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STUDIES IN THE PHYSIOLOGY OF THE NERVOUS SYSTEM. XIV.: IMMEDIATE AND SUCCESSIVE EFFECTS OF COMPOUND STIMULATION IN SPINAL PREPARATIONS. By T. GRAHAM BROWN (Manchester). (With twenty-one figures in the text.)

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# STUDIES IN THE PHYSIOLOGY OF THE NERVOUS SYSTEM. XIV.[1]: IMMEDIATE AND SUCCESSIVE EFFECTS OF COMPOUND STIMULATION IN SPINAL PREPARATIONS.

By T. GRAHAM BROWN (Manchester).[2] (With twenty-one figures in the text.)

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CONTENTS.



[1] The preceding papers have appeared in this Journal: vol. ii., No. 3, p. 243, 1909; vol. iii., No. 1, p. 21, 1910; vol. iii., No. 2, p. 139, 1910; vol. iii., No. 3, p. 271, 1910 (in collaboration with Miss Abel); vol. iii., No. 4, p. 319, 1910; vol. iv., No. 1, p. 19, 1911; vol. iv., No. 2, p. 151, 1911; vol. iv., No. 3, p. 273, 1911; vol. iv., No. 4, p. 331, 1911; vol. v., No. 3, p. 233, 1912; vol. v., No. 3, p. 237, 1912; vol. vi., No. 1, p. 25, 1913; vol. vi., No. 3, p. 209, 1913.

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## I. Introduction.

Spinal preparations in the mammal have been used with comparative rarity in the investigation of the phenomena which accompany the simultaneous combination of antagonistic reflex stimuli, the phenomena which Sherrington has termed those of "double reciprocal innervation."

In the "late" low spinal preparation Sherrington has observed the effects of the compounding of the reflex stimuli which evoke the scratch-reflex and the ipsilateral flexion-reflex of the hind limb; and he has also investigated the effect of interrupting the rhythmic progression movements of the "mark-time" phenomenon by an interposed scratch-reflex. But to the best of my knowledge a systematic study of the effects of the compounding of antagonistic reflex stimuli, applied to afferent nerves peculiar to the hind limbs, has not been made in the low spinal preparation of the mammal.

In the recent high spinal preparation (decapitate cat) Sherrington has, however, observed these phenomena (1). He confines his attention to the phenomena which occur during the period when the two antagonistic stimuli are together in action. During this period there appears an inhibitory relaxation of either the extensor muscle or the flexor muscle, according as either the contralateral extension-reflex or the ipsilateral flexion-reflex is in action before the period of the double reciprocal innervation. In fact, if a reflex be in action, the application of an antagonistic stimulus causes the contractor in the first reflex to relax; and at the same time the relaxor in that reflex may shew a certain amount of excitatory contraction. Where the two antagonistic stimuli used are nearly balanced as regards their strength the relaxation of the previous contractor is often incomplete, while at the same time the contraction of the previous relaxor is not so great as when its evocative stimulus is applied uncomplicated. But where the two stimuli differ considerably in relative strength other effects are obtained. Thus when the interrupting or inhibiting stimulus is comparatively weak there may be little inhibitory relaxation of the previous contractor, while at the same time the previous relaxor may shew no signs of contraction at all. Again, when the interrupting stimulus is comparatively strong there may be produced a complete relaxation of the previous contractor, and at the same time the previous relaxor may exhibit a nearly complete degree of contraction. These effects are obtained when the relative differences of the strengths of the two antagonistic stimuli are conditioned by change either of the strength of the interrupting stimulus (the other then remaining constant in a series of compounded reactions) or by change of the strength of the initial stimulus (the interrupting antagonistic stimulus then remaining of constant strength).

Although Sherrington in that paper confines himself strictly to the phenomena which occur during the period in which the two antagonistic stimuli are in simultaneous being, the tracings reproduced in his figures

demonstrate some of the subsequent effects of the double stimulation. He himself notes that when the stimulus which is interrupted is continued after the withdrawal of the interrupting stimulus, there may occur a restitution of the contraction in the previous contractor (that is, in the muscle which exhibits inhibitory relaxation during double stimulation). His figures shew that this restitution of contraction may in some cases be nearly complete, but that in other cases it may be incomplete—a point which will be examined later in this paper.

This present paper is one of a series in which the phenomena of the compounding of antagonistic stimuli are examined as they occur in muscles which act upon the ankle-joint and in the decerebrate, decapitate, and low spinal preparations of the cat, both in the "normal" and in the "de-afferented" conditions.

In the study of compound reflexes two sets of phenomena are presented. The first of these consists of the happenings during the period in which the two antagonistic stimuli are being applied together. For convenience we may refer to this as the period or phase of "double stimulation"; and the occurrences during it may be termed the "immediate" effects of double stimulation. But after a reflex stimulus has been withdrawn there often occur post-stimulatory ("terminal" or "successive") phenomena, amongst which may be mentioned the positive rebound phenomenon in the relaxor. Such terminal phenomena may be modified on the simultaneous withdrawal of the two antagonistic stimuli at the end of the period of double stimulation; or, if the interrupting stimulus is withdrawn during the continuation of the other stimulus, the terminal phenomena which follow upon that withdrawal may be compounded against, and modified by, the background of the continued stimulus. In the examination of the phenomena of the compounding of antagonistic stimuli there must therefore be included various "successive" effects of the double stimulation. Again, when the interrupted stimulus is continued after the cessation of the period of double stimulation by the withdrawal of the interrupting stimulus, the terminal phenomena which follow upon the cessation of the interrupted stimulus may be found to be modified by the interposition of the interrupting stimulus. This is another of the successive effects of double stimulation which fall to be considered. In this and the following papers of this series an attempt is made to examine some of these "successive" phenomena of the compounding of antagonistic stimuli as well as the immediate effects of that compounding.

In these experiments the two antagonistic stimuli used have sometimes been applied synchronously (or very nearly so), and have again been synchronously withdrawn. But it has been found that much more valuable results are obtained when one of the stimuli is applied in time subsequent to the commencement of the other, and withdrawn again before that other is terminated. This is, as it were, the standard arrangement of stimuli used in these experiments, and within this general arrangement the temporal

relations of the two stimuli have been varied, as well as their relative strengths. A word may be said regarding the nomenclature used.

In a compound reaction where the two antagonistic stimuli are taken in this temporal arrangement four phases are exhibited. The first of these is that in which one of the two stimuli is running alone and it commences with the commencement of that stimulus, and terminates at the point at which the interrupting stimulus is commenced. The second phase, that of double stimulation, commences at the point at which the interrupting stimulus is first applied, and ceases when that stimulus is again withdrawn. The third phase is that in which the first stimulus is still running—now uncomplicated by the presence of the interrupting stimulus—and it ceases at the termination of the first stimulus. There the fourth phase commences. It is that in which the state of the centres again passes back to the condition of "rest." For convenience the stimulus which is first applied and last terminated may be termed the "background" stimulus. The other stimulus is most conveniently called the "interrupting" stimulus. A "pure" or a "simple" reaction is one in which the evoking stimulus is uncomplicated by an interrupting stimulus. In this and in the following papers, where the flexor (or extensor) contraction in a compound reaction is compared with the flexor (or extensor) contraction in a "pure" or "simple" reaction, what is meant in every case is a "pure" or "simple" flexion-reflex (or extension-reflex) evoked at the same strength of ipsilateral (or contralateral) stimulation used in the compound reaction under consideration.

Before passing to the actual results obtained I would like to mention briefly the conditions under which this analysis is made.

It might be thought that the analysis of a series of reflex reactions in which the conditions of the experiment have been suitably varied is one which can be performed almost mechanically, and in which the personal element of the investigator may be almost eliminated. This, unfortunately, is not the case. When a large series of experiments are performed upon the mammal it begins to be seen that there slowly emerge from the background certain marked types of individuality, and often after the first two or three reactions have been recorded in an experiment it is possible to say that the individual leans to this or to that general type. These variations are not due to changing experimental conditions. In part they may possibly be related to the general conditions in the environment obtaining at the time, for it sometimes occurs that in successive series of cats there is much similarity between the individual characteristics—a similarity which cannot be explained as being due to blood relationship, and probably not merely to coïncidence. But these individual variations are probably due in great part to more fundamental differences in the constitution of the nervous centres. Some cats are "walkers." They exhibit in a marked degree the phenomena of "narcosis progression." Other cats are "scratchers." In them the scratch-reflex is peculiarly excitable. In the decerebrate preparations, "rhythmic" cats—where the reflex reactions are

peculiarly phasic; "flexion" cats—where the contraction of the flexor is peculiarly well marked, and where there may be an abnormal crossed flexion-reflex; and "extension" cats—where the contraction of the extensor is peculiarly evident—all appear amongst the individual characteristics. And in addition there are characteristics which are less easily described.

This being so, it is evident that there is scope for much variation in the several phenomena which accompany and succeed a compound stimulation; and there is danger that some of the phenomena may either be stressed too greatly or too little if an end is kept in sight during their analysis. As far as possible to avoid this danger, I have analysed all the compound reactions obtained in the different preparations and conditions before attempting to think of the general bearings of the results.

But now a word may be said regarding the conditions which obtain in a compound reaction.

In the preceding paper of this series the suggestion was advanced that in the simple reflex evoked in response to a simple stimulus there are at work in every case (or in nearly every case) two antagonistic central activities—a flexion activity and an extension activity. So that each "half-centre" (flexor or extensor) at the same time is activated and inhibited by two different central processes. Where the flexion-reflex is evoked the factor of activation overbalances that of inhibition (produced at the same time in the centre by the afferent impulses) in the flexor half-centre, and that of inhibition overbalances activation in the extensor half-centre. The overbalancing occurs in the opposite directions in the two half-centres when the extension-reflex is evoked. The fact that in certain instances of the ipsilateral flexion-reflex as the evoking stimulus is continued there occurs a flexor relaxation accompanied by a reciprocal extensor contraction, and the additional fact that in the contralateral extension-reflex of certain types there is a preliminary transient flexor contraction before the extensor contraction makes its appearance, seem to shew that the two factors vary in relationship with continuation of a simple reflex stimulus. In general, it may be said, at the commencement of a reflex stimulus (ipsilateral or contralateral) the flexion factor—activation of flexor half-centre and depression of extensor half-centre—is at its highest relative value. It holds the field. As the stimulus is continued in time the factor of extension becomes gradually of greater relative value. And in addition to this, it may be said that variation of the strength of the exciting stimulus so acts that the stronger the stimulus the greater is the relative value of the flexion factor.

If this be the case, it is probable that the same two factors condition the terminal phenomena which follow on the cessation of a reflex stimulus. The usual terminal phenomenon in the flexion-reflex (as seen in the antagonists at the angle) is an extensor rebound contraction, and this often persists for many seconds in maintained contraction. After the extension-reflex the usual terminal phenomenon is an extensor "tonic" after-

discharge which carries on the maintained extensor contraction of the reflex. But after the cessation of either reflex there may appear a flexor rebound contraction, which is then often followed by a secondary extensor contraction. It looks as if the same combination of two antagonistic factors conditions the terminal phenomena, and that here, although extension is the dominant one of the two, the flexion factor tends to be relatively at its greatest early in the phenomenon. Upon the whole, it is possible that even in the simple reflex there is a state similar to that of "double reciprocal innervation," and that the equivalent of this is also present in the terminal phenomena of the simple reflex.

This being so, there may be a fourfold combination of factors during double stimulation, and a fourfold combination in the successive phenomena of compound stimulation also. It is therefore possible that the presence of the "background" stimulus may tend to augment the value of its dominant factor in the interrupting stimulus. It might, for instance, be possible that, if a flexion-reflex is in being, a contralateral extension-producing reflex might at first actually give flexor augmentation in the period of double stimulation; and this has been observed to take place in decerebrate preparations. Or, perhaps, if the temporal relations of the two stimuli are such that the interrupting contralateral stimulus falls at a period when the factor of extension in the flexion-reflex is becoming of sufficient relative strength, the interrupting stimulus might condition an extensor contraction greater than that seen in the simple extension-reflex: this has been observed to take place as is here described.

Yet again, on withdrawal of the interrupting stimulus where the background is one of flexion, there may be an augmentation of the flexion factor in the terminal phenomenon of the interrupting stimulus. This might give not only a restitution of the flexion of the background reaction, but even an augmentation of it above that level which is obtained in the simple flexion-reflex: this has been observed in decerebrate preparations. Or the extension factor of the terminal phenomenon might be so great as to cause a relative depression of the flexor restitution of contraction—as more commonly occurs in low spinal preparations. In a similar manner, when the extension-reflex is the background, the withdrawal of the interrupting stimulus might possibly be followed either by a continued depression of extensor contraction, by an exact restitution of it, or by an augmented restitution, so that the level attained is greater than that seen in the simple extension-reflex—all of which phenomena have actually been observed.

## II. Methods Employed.

The methods employed in these experiments have been similar to those already described in previous papers of this series. It is scarcely necessary to say that the cats used have been completely unconscious throughout the experiment and until they were killed at the end of it.

The stimuli used consisted of rapid faradic shocks applied for varying intervals of time. Short circuit keys were not used in the secondary circuits. In each secondary circuit the two wires leading to the electrodes had each, between electrode and coil, a make and break key. In each secondary circuit these two keys were simultaneously closed at the commencement of stimulation and opened at its termination. A third key, simultaneously closed and opened, was in the signal circuit. When a nerve was not being stimulated there was therefore no metallic connexion between its electrodes and the secondary coil.

The two secondary coils used were arranged upon one primary coil. As the physical conditions in the two secondary circuits change with the varying resistances in them (when the nerve is placed in and out of circuit), and as the change in the resistance in one circuit affects the value of the current in the other secondary circuit, a few experiments were performed with fresh dead nerves in one secondary circuit. It was found that the change in value of the current in the live nerve circuit when the other was thrown open was negligible.

Another point which may be noted is the behaviour of the ankle extensor used in these experiments. This muscle, which I have usually described as "gastrocnemius," is really gastrocnemius-soleus. As gastrocnemius itself arises in part from the lower portion of the femur it might possibly act as a knee flexor, and such phenomena as the late extensor contraction seen in some forms of flexion-reflex might be thought to be really a late knee flexion mediated by gastrocnemius as a knee flexor. That this is not the case is shewn by the occurrence of the same phenomenon when soleus only is used, for that muscle arises from the tibia alone. Experiments in which the movements of gastrocnemius and of soleus have been recorded separately at the same time shew that the two muscles behave in a similar manner—that is, as extensors. They both shew such phenomena as "extensor rebound contraction after excitation" in the crossed extension-reflex. A curious point noticed has been a difference in their thresholds of excitability in the contralateral extension-reflex—an observation which perhaps needs more exact confirmation.

## III. Low Spinal Preparation—Immediate Effects.

### A. Stimuli of Synchronus Commencement.

When ipsilateral and contralateral stimuli are commenced and terminated at the same instants of time, the resultant reaction may be compared with the simple ipsilateral and contralateral reactions obtained immediately before or immediately after the compounded reaction. But this method of demonstrating the immediate effects of the compounding of stimuli is not so good a one as that in which the one stimulus is commenced in time before the other, and in which the compounded part of the reaction may be compared with the first part—where the reaction is one in response to

a "simple" stimulus. For this reason comparatively few reactions in which the two stimuli commence and end simultaneously have been registered.

In these cases of low spinal reactions of "spinal" form it has invariably been found that when the two antagonistic stimuli have been commenced synchronously, the contraction of the flexor muscle is smaller than in simple reactions in which the ipsilateral stimulus is of the same strength. This reduction of the flexor contraction may even occur when there is no reaction of extensor contraction evoked by the contralateral stimulus—a condition frequently found in the low spinal preparation. It usually takes the form of a diminution of the extent of the initial flexor contraction and a diminution of the height of the ensuing plateau of maintained contraction. In some cases there may be a comparatively small diminution of the initial contraction and a very rapid fall of the curve during the remaining portion of the period of stimulation. This may result in the disappearance of the state of contraction even during the period of stimulation, although no such effect is seen in the case of the "simple" ipsilateral reaction at the same strength of stimulus. The depression of the flexor contraction may be so great that from the commencement there is complete abolition of it. This occurs when the ipsilateral stimulus is relatively weak and the contralateral relatively strong.

The movements of the extensor muscle during simultaneous ipsilateral and contralateral stimulation are of interest. In these records it has been found that often there is an augmentation of the extensor contraction—a somewhat unlooked-for result. It may occur that there is no reaction in response to the simple contralateral stimulus, and that there is no extensor contraction in the flexion-reflex, but that when the two stimuli are applied at the same time there appears an extensor contraction (fig. 6). In such a case the extensor contraction appears late in the period of stimulation, although then it may be well marked. The reaction then seems much to resemble the simple ipsilateral flexion-reflex of "decerebrate" type.

Even when there is present a simple contralateral extension-reflex the extent of the extensor contraction may be augmented during the simultaneous application of the two antagonistic stimuli. In such cases it is usual for there to be a great increase in the latency of the extensor contraction, although when that contraction appears it is greater, and sometimes markedly greater, than usual.

Occasionally the extent of the contraction of the extensor is not increased, but is diminished or abolished when the two antagonistic stimuli are applied together (fig. 1). This has been observed to occur when the ipsilateral stimulus was a weak one, although in these cases the contralateral was also weak.

Sometimes it happens that the extensor contraction during double stimulation is markedly rhythmic. An instance of this has already been published (2), and these rhythmic phenomena will be discussed in a later paper of this series.

On one or two occasions in experiments in which the low spinal simple reflexes were of "spinal" form, series of reactions have been recorded when the antagonistic stimuli have been of different strengths (fig. 2).

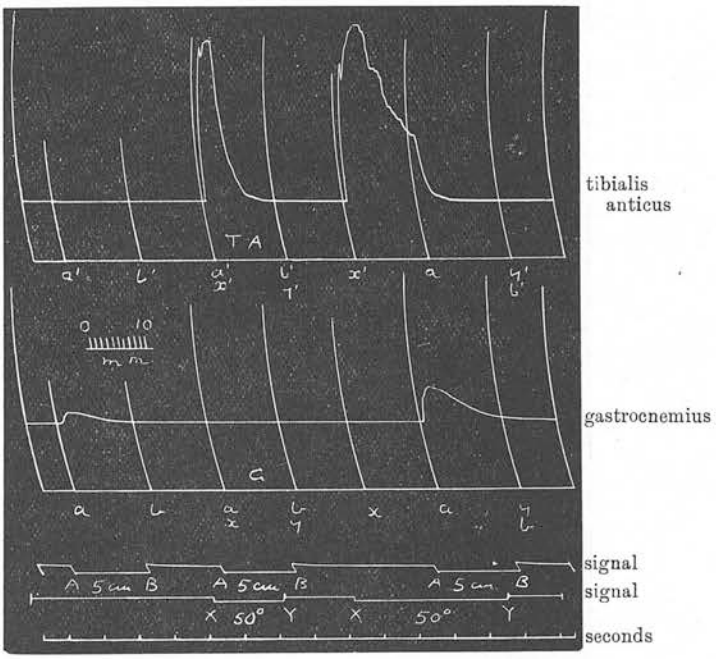


FIG. 1.—Experiment C, xxxii., record 57, 1518; 7/4/11.—Low spinal cat, a reaction obtained 7 hours and 21 minutes after division of the spinal cord. A contralateral stimulus is first applied and evokes a slight extensor contraction. Then, 2 seconds later, an ipsilateral and a contralateral stimulus are synchronously applied. There is, in the compound reaction, no element of extensor contraction. Two seconds after this an ipsilateral stimulus is given, and after it has run for 2 seconds a contralateral stimulus is added to it. During the period of double stimulation there is a marked extensor contraction which is greater than in the first "pure" contralateral reaction. The flexor contraction before double stimulation is here seen to be greater than that in the previous reaction.

This shews depression of flexor contraction during double stimulation; complete abolition of extensor contraction during double stimulation when the two stimuli are applied together; and augmentation of extensor contraction when the contralateral stimulus is first applied later in the period of double stimulation.

In this and in the following figures the rise of a curve denotes contraction of a muscle, and the fall denotes relaxation. The upper tracing is obtained by registration of the movements of the flexor (tibialis anticus), and the lower by registration of the movements of the extensor (gastrocnemius). Below the muscle curves are two signal lines. Of these the upper registers the commencement and termination of contralateral stimuli. The points are marked by the letters "A" and "B." Corresponding ordinates (marked $a$, $a'$; $b$, $b'$) are drawn upon the two muscle curves. The lower signal similarly registers ipsilateral stimuli —the letters used being "X" and "Y"; and the corresponding ordinates being lettered $x$, $x'$; $y$, $y'$. [These corresponding ordinates are only approximately correct.] Between the letters on the signal lines are figures which give the relative values of stimulation in centimetres distance of primary and secondary coils—or sometimes in degrees of rotation of the secondary from the axis of the primary when the coils are set at 17 cm. distance apart. Numbered ordinates have in some cases been drawn upon the muscle curves to mark other time relations than those of stimulation. On the curves millimetre scales have been drawn before the tracing was varnished; these are therefore reduced in proportion to the tracings in reproduction. Time is marked in seconds upon the lowest line.

[From the same experiment as figs. 2, 6, 8, and 12.]

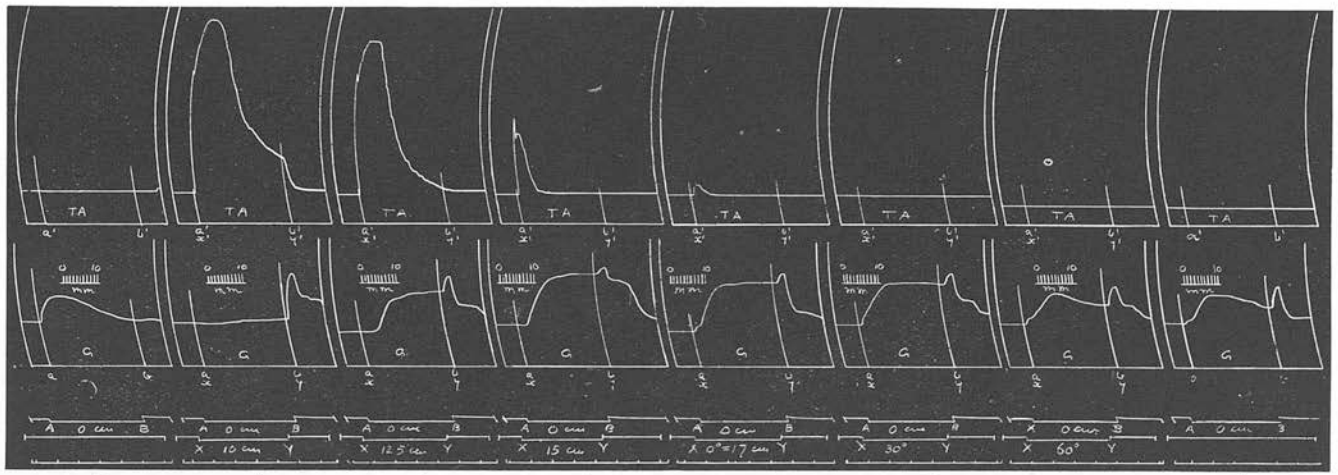


FIG. 2.—Experiment C, xxxii., record 57,1523; 7/4/11.—Low spinal cat, a series of reactions obtained 7 hours and 43 minutes after division of the spinal cord. The reactions are taken at intervals of 2 minutes each. The first and last of the series are "pure" contralateral extension reactions. The intervening reactions are compound, and are obtained by synchronous ipsilateral and contralateral stimulation. Throughout the series the contralateral stimulus remains of constant value, but the ipsilateral stimulus is successively decreased in value.

It will be seen that when the ipsilateral stimulus is strong (reaction *b*) there is almost complete suppression of extensor contraction during double stimulation. As the ipsilateral stimulus is weakened this appears and even becomes of greater extent than in the "pure" contralateral reactions. The extensor contraction then again is reduced with further reduction of the value of the ipsilateral stimulus. That the extensor augmentation during double stimulation is not due to an increase in the excitability of the "pure" extension-reflex is shewn by the fact that in the last reaction that is little different from the extension-reflex in the first reaction. It will be seen also that an element of extensor rebound contraction makes its appearance and is augmented after the cessation of double stimulation.

[From the same experiment as figs. 1, 6, 8, and 12.]

In these instances the contralateral stimulus was of constant strength, and the strength of the ipsilateral was either decreased or increased in successive reactions. It was found that, if the ipsilateral stimulus was at first of great strength and was then gradually decreased, in the first compounded reaction there might be a complete abolition of the extensor contraction. At the same time there was a reduction of the flexor contraction in extent and maintenance. In the following reactions (taken with decreasing strengths of flexion-producing stimuli) the extensor contracted during the period of compounded stimulation. The commencement of this contraction was at first of long latency; but as the strength of ipsilateral stimulus was still further decreased the latency became shorter and at the same time the extent of the extensor contraction increased and was greater than that in the "pure" extension-reflex. The flexor contraction became smaller, and finally was abolished at a strength of ipsilateral stimulation which, if applied uncompounded, gave a fair flexion-reflex. About this point in the series (or in the preceding reaction) the extensor contraction reached its maximum, and in the succeeding reactions —where the ipsilateral stimulus was still further decreased in strength —the extensor contraction became less in extent. It was, however, still greater than in a "pure" contralateral reaction of the same strength (unaltered throughout the series). Contralateral reactions obtained before and after the series were almost similar in extent of extensor contraction.

### B. Stimuli of Asynchronous Commencement; beginning with the simple Ipsilateral Flexion-Reflex.

In many cases the two antagonistic stimuli used have not been applied at the same time. In these experiments it is not only possible to examine the immediate effect on a "simple" reaction of compounding it with an antagonistic one, but it is also possible to investigate the effect of compounding two antagonistic stimuli at different intervals of time after the commencement of one of them. It is clear that the reaction may be made to commence either with "simple" extension or with "simple" flexion.

Of these reactions, we may consider in the first place the reactions in which the temporal relations of the two stimuli are unaltered in series of reactions. The strength of stimulus then remained in one case unaltered, and in the other case progressively increased or decreased.

In those instances in which the contralateral stimulus remained of constant value, but in which the ipsilateral was progressively changed in succeeding reactions, the results confirm the observation above, that there is a depression of the flexor contraction, and often an augmentation of the extensor even above that seen in the "simple" contralateral extension-reflex of a similar strength of stimulation. Strong ipsilateral stimuli produced abolition of the extensor contraction; weaker, however, gave

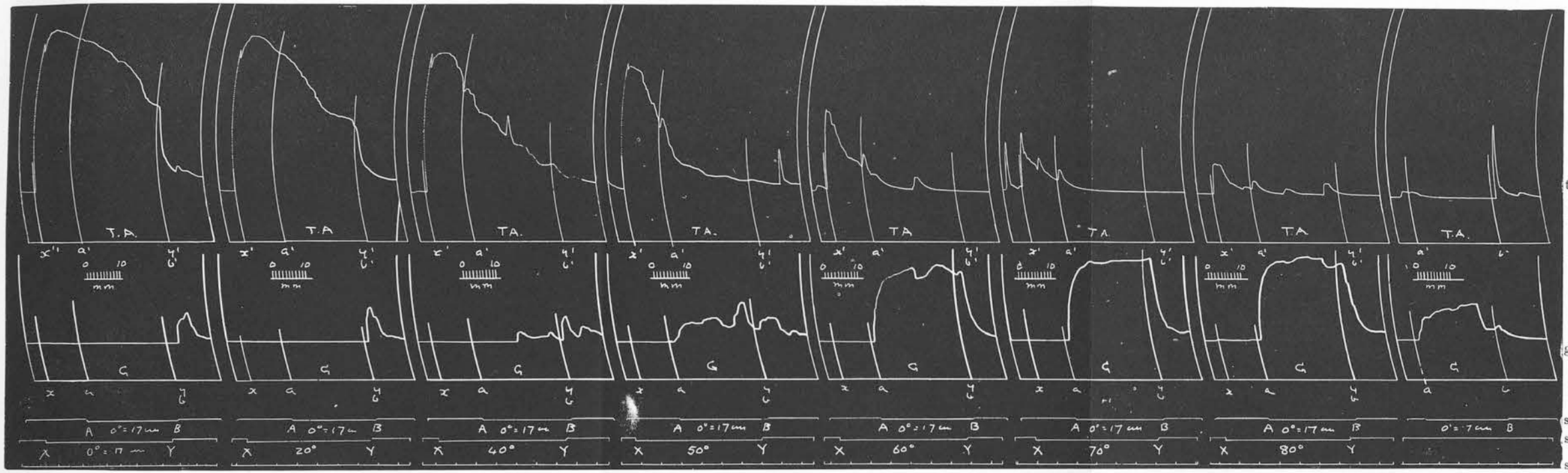


FIG. 3.—Experiment C, xxxi., record 55, 1420 ; 5/4/11.—Low spinal cat, a series of compound reactions obtained 5 hours and 55 minutes after division of the spinal cord. The reactions are taken at minute intervals, and under the same conditions as in the preceding figure (which, however, is from a different experiment). The ipsilateral stimulus here is commenced in each case 2 seconds before the contralateral. With strong ipsilateral stimuli there is complete abolition of the extensor contraction during double stimulation ; with weaker ipsilateral stimuli (reaction *c*) extensor contraction is of long latency and is reduced in comparison with that of a "pure" extension-reflex of the same strength of stimulus (reaction *h*) ; further reduction of the value of ipsilateral stimulation gives an irregularly rhythmic extensor contraction (reaction *d*); then, in reactions *e, f, g,* there is actual augmentation of extensor contraction as compared with the "pure" reaction in *h*. It will be seen that in the early reactions of this series there is an extensor rebound contraction on cessation of double stimulation. Just before the commencement of this series a "pure" contralateral reaction of the same strength of stimulation as that used throughout the series gave a reaction almost exactly similar to that in reaction *h* ; the height of extensor contraction was slightly greater, there was a slight preliminary flexor contraction, and there was no flexor rebound contraction on cessation of stimulation.

augmentation. In these instances the contralateral stimulus was made to commence about two seconds after the ipsilateral, and it was found that the augmentation of extensor contraction persisted with the weakest ipsilateral stimuli used. The extensor augmentation was such that the extent of contraction was considerably greater than that which obtained in the "simple" contralateral extension-reflex (fig. 3). Even when the contralateral stimulus when applied alone gave no reaction at all, it has been observed not only that there was an inhibitory relaxation of the flexor contraction when the contralateral stimulus was applied during the ipsilateral, but also that there might be an extensor contraction. This extensor contraction was only obtained when the ipsilateral stimulus was weak.

In only two instances has the strength of the ipsilateral stimulus been kept constant, and that of the contralateral progressively changed. In one case it was found that with progressive weakening of the contralateral stimulus (which was commenced two seconds after the commencement of the ipsilateral) the extensor contraction increased in extent to a maximum and then decreased with progressive decrease of the contralateral stimulus. In the other case, with progressive strengthening of the contralateral stimulus there occurred an ever greater flexor relaxation and extensor contraction. Weak contralateral stimulation in the compound reaction conditioned no extensor contraction during double stimulation, but there was flexor relaxation. Stronger contralateral stimuli gave extensor contraction which, at its maximum, was of greater extent than in the simple contralateral reflex evoked at that strength of contralateral stimulus.

Secondly, we may look at the effects of change of the temporal relations of the two stimuli. In these cases the strengths of the two antagonistic stimuli have remained unchanged, but the contralateral stimulus has been applied at ever greater (or ever shorter) intervals of time after the commencement of the ipsilateral stimulus.

When a contralateral extension-reflex is applied during the application of an ipsilateral flexion-reflex, in general the flexor contraction is reduced. The extent of this reduction may be complete when the strength of the contralateral stimulus is great, but more often it is partial only. In such cases it is usually found that the effect is greater the later the commencement of the contralateral stimulus falls after the commencement of the ipsilateral (figs. 4, 5). This may be observed when there is no extensor contraction in the period of double stimulation.

In a similar manner it is found that often the contraction of the extensor muscle (when that occurs during double stimulation) is greater the later the contralateral stimulus commences after the commencement of the ipsilateral. This may be demonstrated in a single reaction by first applying the contralateral stimulus alone, then applying contralateral and ipsilateral simultaneously, and finally first applying the ipsilateral and then commencing the contralateral later in the period of stimulation (fig. 1).

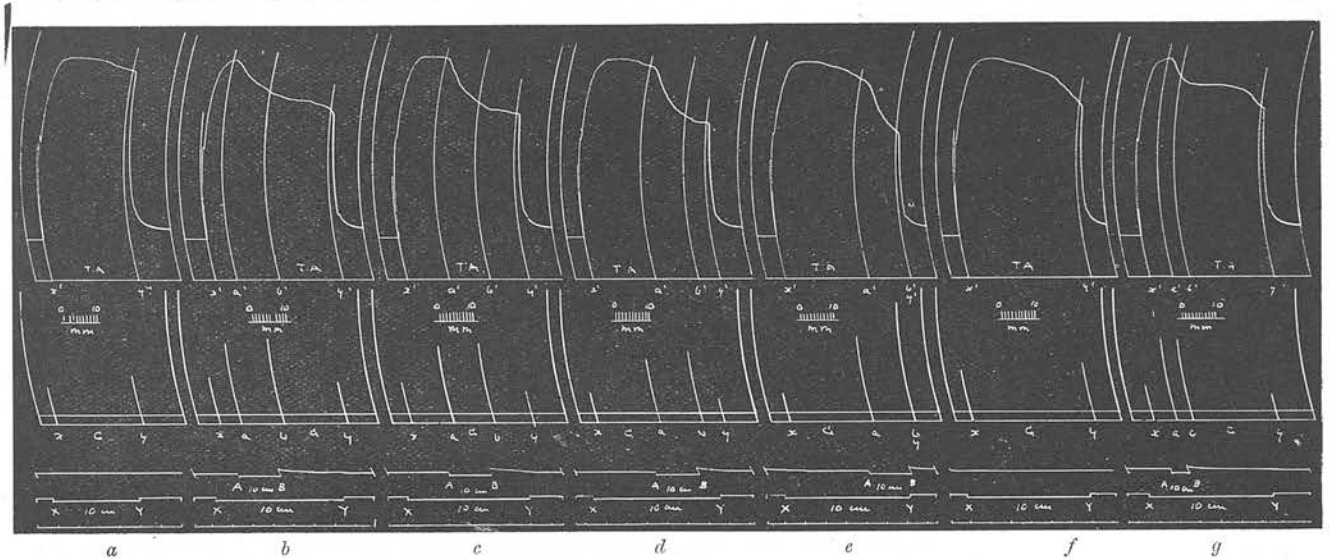


FIG. 4.—Experiment C, xxix., record 52, 1288; 30/3/11.—Low spinal cat, a series of compound reactions obtained 4 hours and 7 minutes after division of the spinal cord. The several reactions are taken at minute intervals. Here the ipsilateral stimulus (of unchanged strength throughout) serves as the "background" stimulus. It is applied for periods of 6 seconds, and reactions *a* and *f* are "pure" ipsilateral reactions. An interrupting contralateral stimulus—also of constant strength throughout the series—is applied for periods of 2 seconds (except in reaction *g*, where it is applied for 1 second only) at different intervals after the commencement of the ipsilateral "background" stimulus. The intervals are :—*b*=1 second, *c*=2 seconds, *d*=3 seconds, *e*=4 seconds. In *g* the interval is again one of 1 second.

This series shews a greater depression of flexor contraction during double stimulation the later the contralateral stimulus falls in the period of ipsilateral stimulation. The following flexor depression after double stimulation is seen also to be greater under these conditions. On comparing *b* and *g*—where the interval is 1 second but the contralateral stimulus is not applied for the same length of time—the subsequent depression is seen to be greater the longer the contralateral stimulus is applied—that is, in *b*.

Compare with figs. 5 and 11, where the outlines obtained from these curves are superposed.

[From the same experiment as figs. 5, 11, and 16.]

In these circumstances it may happen that the strength of ipsilateral stimulation is sufficient to abolish the contraction of the extensor when both stimuli are applied together, but that when the ipsilateral stimulus is allowed first to run alone for two seconds, the contralateral stimulus, besides giving relaxation of the flexor, gives a contraction of the extensor which is actually greater than that in the "simple" reflex.

When the commencement of the contralateral stimulus is applied in series at ever greater intervals of time the latency of extensor contraction

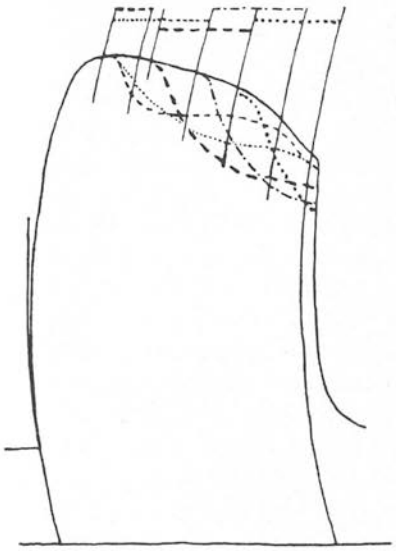

FIG. 5.—This figure is one obtained from the previous one by tracing the outlines of the several reactions *b*, *c*, *d*, *e*, and *g* together over the outline of the "pure" reaction *f*. The different outlines are differently marked (dots, broken lines, etc.), and the ordinates between which the several contralateral stimuli were applied are also drawn in and joined together by horizontal lines (differently marked in correspondence with the different outlines of the reactions) for clearness of comparison.

This figure demonstrates more clearly that, upon the whole, there is a greater depression of flexor contraction during double stimulation the later the contralateral stimulus falls, and that the subsequent depression is also greater.

decreases, and the rapidity with which the maximum contraction is attained increases, the later the contralateral stimulus is applied. At the same time the maximum extent of contraction may increase, although in other cases it may remain constant. When the interval which elapses between the commencement of the ipsilateral flexion-reflex and the contralateral extension-reflex is varied in successive reactions between the extremes of one and fifteen seconds (say), it may be found that a maximum effect of extensor contraction is attained at a certain interval, and that with shorter or longer intervals the extensor contraction is less (fig. 6). With the shorter intervals of time the latency of extensor contraction is

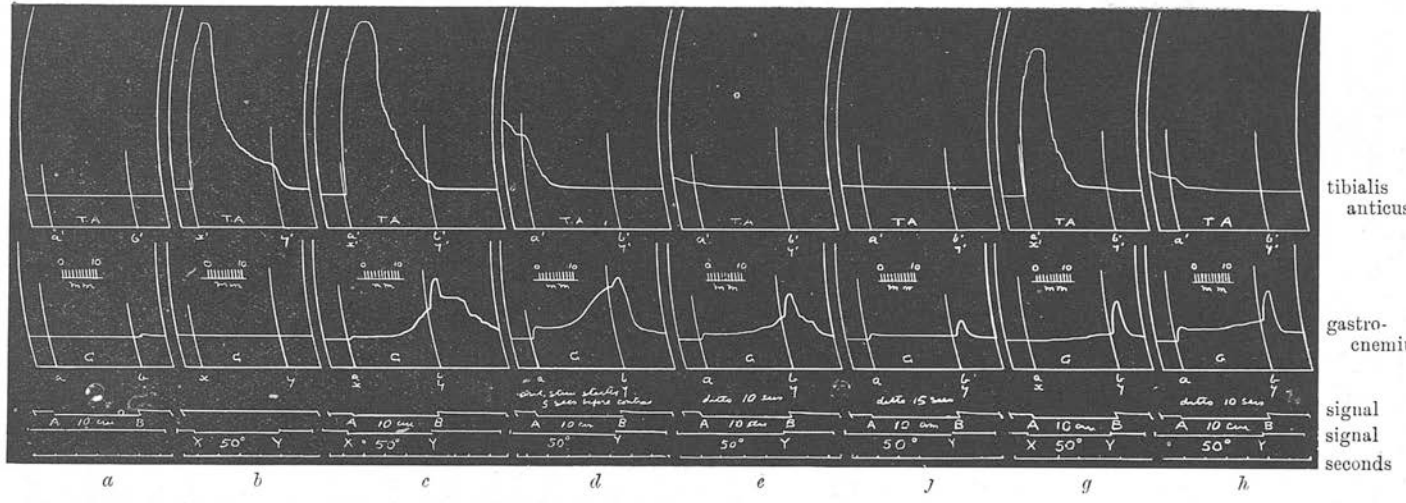


FIG. 6.—Experiment C, xxxii., record 57, 1504; 7/4/11.—Low spinal cat, a series of compound reactions obtained 6 hours and 55 minutes after division of the spinal cord. The reactions are taken at minute intervals, except that an interval of 4 minutes elapses between reactions *b* and *c*, and one of 5 minutes between *g* and *h*.

Reaction *a* is a "pure" contralateral extension-reflex. But no contraction occurs during stimulation, and there is only a slight extensor rebound contraction after stimulation has ceased. Reaction *b* is a "pure" ipsilateral flexion-reflex. The other reactions are all compounded of these two reflexes. In *c* and *g* the stimuli are synchronous. In the remaining reactions the ipsilateral stimulus is first commenced—in *d*, 5 seconds before the commencement of the contralateral; in *e* and *h*, 10 seconds; and in *f*, 15 seconds.

This series shews extensor augmentation during double stimulation. With the synchronous stimuli there is a slight extensor augmentation which increases late in the period of double stimulation. As the contralateral stimulus is applied later in the period of the ipsilateral stimulus the extensor contraction during double stimulation is found to be greater, but with still later contralateral stimuli it again decreases. There is an increase of the extensor rebound contraction.

[From the same experiment as figs. 1, 2, 8, and 12.]

greater. As the intervening interval is increased the latency decreases and the extent of the extensor contraction increases, so that it may sometimes be greater than in the "simple" reaction. After the maximum is reached and passed the extent gradually decreases, but the latency remains short. In records in which the interval is one of fifteen seconds the extent of extensor contraction may still be greater than normal.

### C. Stimuli of Asynchronous Commencement; beginning with the Simple Contralateral Extension-Reflex.

In these instances it has been observed that the flexor contraction during the phase of double stimulation in the compound reaction was smaller in extent than in the simple flexion-reflex. Where the two stimuli were applied at the same time the flexor contraction was greater than in reactions in which the ipsilateral stimulus was applied one second after the commencement of the contralateral. But thereafter an increase in the interval between the commencements of the two stimuli was accompanied by an increase in the extent of the flexor contraction, although that did not attain to the normal extent. This has been observed in instances in which the "simple" contralateral stimulus gave no evident extensor contraction, but later in the experiment gave the abnormal crossed flexion-reflex. When the ipsilateral stimulus is strong, and the contralateral gives an extensor contraction, that may be completely abolished. If the strength of the ipsilateral stimulus be then decreased, an initial depression of the extensor contraction may be succeeded by a restitution of contraction during the period of double stimulation. Even when the "simple" ipsilateral stimulus gives no phase of extensor contraction late in the period of stimulation, when it is applied during the contralateral extension-reflex there may be a marked phase of extensor contraction. This may be preceded by preliminary extensor relaxation; and the secondary extensor contraction during double stimulation may be of greater extent than that of the extensor contraction in the simple extension-reflex (fig. 8, reaction *e*).

Comparatively few observations have been made in the low spinal preparation when the extension-reflex precedes in its commencement the flexion-reflex. The tendency for the extensor contraction soon to die out in this state if the exciting stimulus be long continued makes it difficult to obtain good results.

### D. Where the Reflexes are of "Decerebrate" Type.

Although the "decerebrate" types of extension and of flexion-reflexes may occur in the low spinal preparation, they are rarer than in the decerebrate preparation itself, and when present are usually not of so well-marked characteristics. Thus in the flexion-reflex the flexor contraction may shew the typical weakening during stimulation without a corresponding extensor contraction making its appearance (although that

may appear). We may leave the question of the "decerebrate" form of flexion-reflex aside. In these experiments an extension-reflex of "decerebrate" type has upon one occasion been compounded with a flexion-reflex of "spinal" type. The compounding of the two stimuli was arranged in different reactions in different temporal orders (fig. 8).

Here the "simple" contralateral extension-reflex exhibited a preliminary extensor contraction which soon again relaxed and was then reciprocally accompanied by flexor contraction. This was transient, and when the flexor contraction disappeared the extensor contraction again rose and remained maintained until the end of the period of stimulation, when cessation of stimulation was followed by an extensor rebound contraction after excitation.

It was then found that, with the strengths of stimulation used, if the flexion-reflex was applied during the application of the extension-reflex and when the extensor was in a state of maintained contraction, the flexor contraction during the period of double stimulation fell rapidly from its initial height. The extensor exhibited a phase of relaxation in the first part of the period of double stimulation, and this then gave place again to contraction which might even be greater than was the extensor contraction before the commencement of the flexion-reflex.

On the other hand, when the contralateral extension-reflex was applied during the period of flexion stimulation, the flexor contraction gave place to relaxation, and the extensor exhibited a phase of contraction. This did not exhibit the secondary relaxation and reconstitution of the "decerebrate" type, but at once rose in the ordinary manner to its full extent and thereafter remained in level maintained contraction for the remainder of the period of stimulation.

### IV. Low Spinal Preparation—Successive Effects.

When two antagonistic stimuli are compounded together in different combinations of temporal relationship, the phenomena which follow the withdrawal of stimulation—the terminal reflex phenomena—may be examined in five different states. In the first place, the two stimuli may be stopped synchronously; in the other cases the one stimulus may be withdrawn before the other, so that the transition from the state of double stimulation to that of absence of stimulation is attained, as it were, in two steps. Thus, secondly, the extension-reflex may be stopped while the flexion-reflex is still running, and the terminal phenomena may then be considered both in the phase after the extension-reflex has been stopped and before cessation of the flexion-reflex, and in the phase immediately after the cessation of the flexion-reflex. Thirdly, the flexion-reflex may be stopped before the extension-reflex, and in this case too the same two steps occur and the terminal phenomena may be again considered in two phases—that in which the flexion-reflex has stopped

but the extension-reflex still is in process, and that after cessation of the extension-reflex. Fourthly and fifthly, interesting variations of these last two are those in which the two stimuli are not commenced synchronously, but one commences after the other and is continued after the cessation of the other. In these two types two steps lead up to, and two down from, the state of double stimulation.

### A. Stimuli of Synchronous Termination.

When the two compounded stimuli are synchronously stopped the terminal phenomena have been observed in these experiments only when there was a terminal contraction.

Where there is no extensor terminal contraction ("rebound contraction") either in the flexion-reflex or in the extension-reflex, there may yet appear such a terminal contraction when both stimuli of a compound stimulation are synchronously stopped (fig. 12). This has been observed when the contralateral stimulus when given alone gave no reaction, and when in the compound reflex there was no factor of extensor contraction. The terminal contraction then was found to increase in extent with increase in the strength of the contralateral stimulus. The effect of this stimulus during the period of double stimulation was observed in an inhibitory relaxation of the flexor contraction of the flexion-reflex.

When there is an extensor terminal contraction in the simple flexion-reflex this may be found to be augmented when the flexion and extension reflexes are compounded and both stimuli synchronously stopped (fig. 3).

Of especial interest are the cases in which there is an extensor terminal contraction after the contralateral extension-reflex, and in which the double stimulation (ipsilateral and contralateral) is accompanied by a marked extensor contraction.

The extensor terminal contraction may then be very markedly augmented when, after a double stimulation, both stimuli are stopped synchronously. This has been noticed in series in which the contralateral stimulus has been applied at ever greater intervals of time after the commencement of the ipsilateral—although both have been terminated synchronously (fig. 6). It may then be found that although there is little or no extensor contraction during stimulation when the two stimuli are made both to begin and to end synchronously, there may yet be a marked extensor terminal contraction. As the contralateral stimulus is then applied at ever greater intervals of time after the commencement of the ipsilateral, the immediate extensor contraction increases in extent. But the terminal extensor contraction may not then increase in height. Relatively to the extent of maintained extensor contraction at the moment of cessation of stimulation, this terminal contraction may appear reduced; but relatively to the abscissa it remains of constant height (or it is very slightly reduced). As the interval of time which is allowed to elapse between the

commencements of the two stimuli is made greater, the extent of immediate extensor contraction begins again to decrease, and with this there is a gradual decrease in the extent of the terminal contraction. It must be remembered that with an increase in the duration of a simple flexion-reflex there would be expected to occur a decrease in the extensor terminal contraction. But even although this decreases it does not diminish to the size of the extensor terminal contraction of the extension-reflex—whereas there may be no extensor terminal contraction of the simple flexion-reflex (fig. 6). When the strength of ipsilateral stimulation is changed in successive compound reactions the extent of the extensor terminal contraction may not markedly change (fig. 2). This may occur even when there is a marked augmentation of it as compared to a terminal extensor contraction of a simple extension-reflex ("extensor rebound contraction after excitation"). Thus with a contralateral stimulus of a certain value (not changed throughout the series) and with an ipsilateral stimulus of a certain other value there may be during double stimulation no immediate extensor contraction, but a marked extensor terminal contraction on cessation of stimulation. With a weaker ipsilateral stimulus there may appear an immediate extensor contraction during double stimulation, but the terminal contraction may appear to be of the same extent as before; and the same may be the case when the immediate extensor contraction is still greater—the ipsilateral stimulus being still weaker. This seems to indicate that the constant contralateral stimulus is here the greater factor in the production of the extensor terminal contraction, even although that contraction is greater than in the simple extension-reflex.

### B. Stimuli of Asynchronous Termination: Contralateral Extension-Reflex left in Action.

In the low spinal preparation this form of the combination of two antagonistic stimuli has but rarely been investigated, because it is rare (at any rate in the preparations I have used, and in the muscles at the ankle) for an extension-reflex of sufficient sustentation to be obtained. It has, however, occasionally been examined.

In few cases was the extension-reflex well maintained. In one of these (fig. 7) it was found that an ipsilateral stimulus, when applied during the contralateral extension-reflex and terminated before the termination of that reflex, gave relaxation of the immediate extensor reflex contraction during the phase of double stimulation. On termination of the ipsilateral stimulus the extensor contraction was again established. The ipsilateral stimulus was commenced two seconds after the commencement of the contralateral. If it was of brief duration—two seconds—the reëstablishment of the extensor contraction was to the same level that obtained before the period of double stimulation. There was, however, a slight extensor "rebound" contraction before the level of maintained contraction was

assumed. On termination of contralateral stimulation the extensor contraction died down without any terminal contraction in either muscle. When the period of ipsilateral stimulation during the extension-reflex was

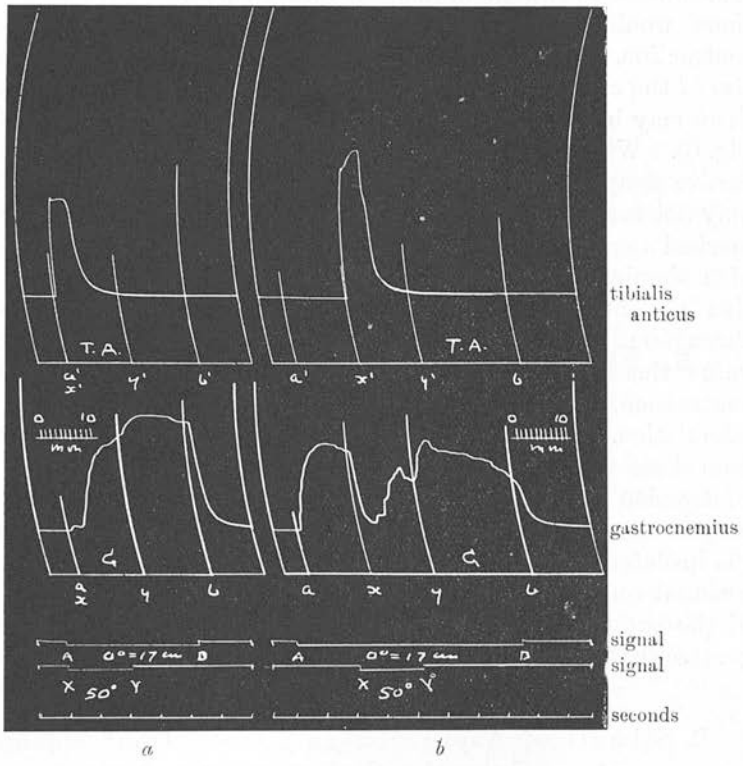


FIG. 7.—Experiment C, xxx., record 54, 1375 ; 31/3/11.—Low spinal cat, two reactions obtained 3 hours and 56 minutes after division of the spinal cord. The reactions are compounded at the same strengths of ipsilateral and of contralateral stimulation, but the temporal arrangements of the two stimuli differ. An interval of 1 minute elapses between them.

In reaction *a* the two stimuli are commenced synchronously, and the ipsilateral is withdrawn during the running of the contralateral. The extensor contraction is retarded and depressed during double stimulation (in the first part of reaction *b* the contralateral stimulus is "pure," and may be used for comparison). On removal of the ipsilateral stimulus there is an augmentation of extensor contraction to an extent greater than in the "pure" reaction.

In reaction *b* there is a greater flexor contraction during double stimulation than in *a*. The ipsilateral stimulus is applied 2 seconds after the commencement of the contralateral, and again withdrawn 2 seconds before the termination of the contralateral stimulus. There is a greater depression of extensor contraction during double stimulation—as seen, for instance, at the end of the 2 seconds of double stimulation. On cessation of the ipsilateral stimulus there is a slight and transient extensor augmentation. In this case, therefore, the value of flexion in the period of double stimulation is greater where the ipsilateral stimulus is applied late in the period of contralateral stimulation.

of greater duration—six seconds—the restitution of extensor contraction after the termination of ipsilateral stimulation failed to attain to the level which obtained before the commencement of that stimulation, and the extensor contraction then died away during the continued contralateral stimulation. If the two stimuli were applied at the same time, but the

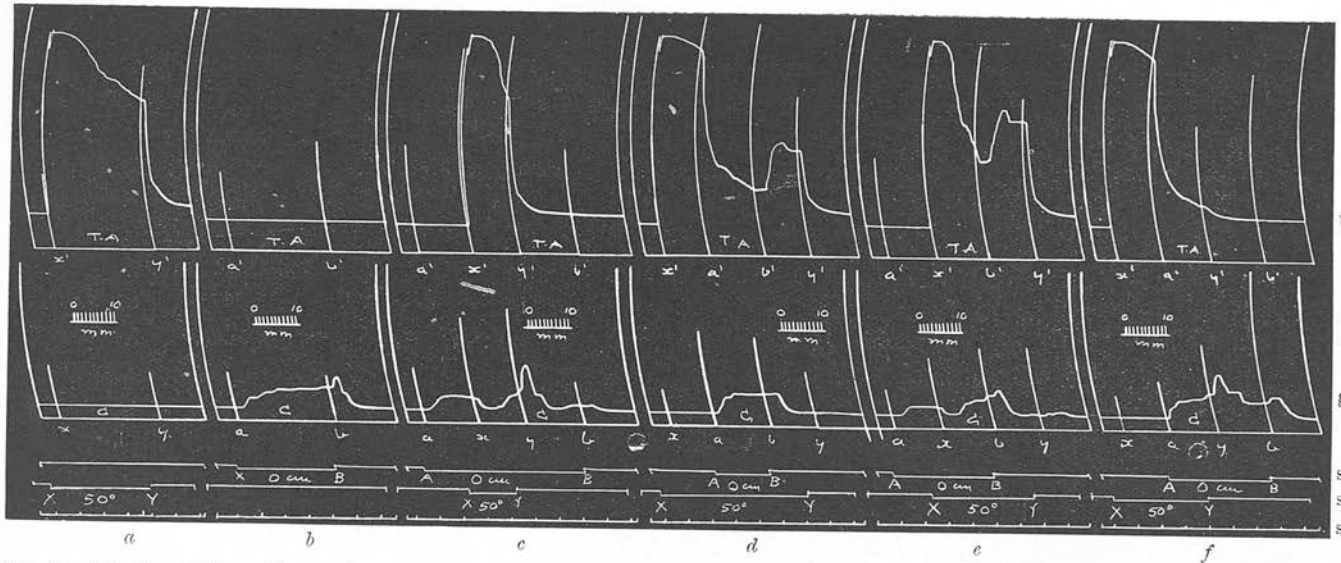


FIG. 8.—Experiment C, xxxii., record 56, 1469 ; 7/4/11.—Low spinal cat, a series of compound reactions obtained 5 hours and 5 minutes after division of the spinal cord. The reactions are separated by minute intervals. Reactions *a* and *b* are in response to "pure" ipsilateral and contralateral stimuli respectively. The other reactions are obtained by compounding these in different arrangements but at the same strengths of stimulation.

In reaction *c*, against an extension "background," the ipsilateral stimulus gives first relaxation and then reconstitution of extensor contraction during double stimulation. Withdrawal of it is followed by an extensor rebound-like contraction followed by a later depression during the continuation of the contralateral stimulus. In *d* the temporal relations of the stimuli are reversed. Depression of flexor contraction occurs during double stimulation, and on withdrawal of the contralateral stimulus there is a certain degree of flexor restitution of contraction.

Compare reaction *c* with reaction *d*. In both the period of double stimulation is of the same length of time—2 seconds ; and in both the values of the stimuli used are the same. But during double stimulation in *c* the flexor contraction is much greater than in *d*, and this relative greatness persists through the whole period, so that at the end of it there is a greater flexor contraction in *c* than in *d*. Conversely, the extensor is more depressed in *c* than in *d*.

Reactions *e* and *f* are in "step" arrangement. Reaction *e* up to the end of double stimulation is similar to reaction *c* ; but double stimulation is terminated by the withdrawal of the contralateral and not of the ipsilateral stimulus. During the further running of the ipsilateral stimulus there is a partial reconstitution of flexor contraction which is greater than that in reaction *d*. An extensor rebound contraction at the end of the period of double stimulation if present is slight in extent. On the other hand, reaction *f* is similar to reaction *d* up to the end of double stimulation—where the contralateral stimulus and not the ipsilateral is continued. During the continuation of the contralateral stimulus there occurs a further depression of flexor contraction, and a well-marked extensor rebound contraction is followed by a more sustained extensor maintained contraction than in reaction *c*—where also the contralateral stimulus is carried on after double stimulation.

From this and similar experiments it may be inferred that in the ipsilateral flexion-reflex (or contralateral extension-reflex) the value of flexion (or of extension) is greatest immediately after the commencement of the stimulus and then gradually wanes ; so that a contralateral stimulus (or an ipsilateral) has—within limits—a greater effect the later it is applied after the commencement of an ipsilateral stimulus (or of a contralateral), and the restitution of flexion (or of extension) is greater the earlier the interrupting stimulus is applied and taken off again.

[From the same experiment as figs. 1, 2, 6, and 12.]

ipsilateral withdrawn after two seconds and when the contralateral stimulus was still running, the extensor contraction was augmented after the withdrawal of the ipsilateral stimulus (fig. 7). This augmentation was to an extent greater than that which obtained in the "simple" extension-reflex. On termination of the contralateral stimulus the extensor contraction at once fell without any terminal contraction in either muscle. (In this experiment there was a rhythmic phenomenon in the extensor muscle during the period of double stimulation—a phenomenon which will be described in greater detail in a later paper.)

In a second instance (fig. 8) there was a slight extensor terminal contraction after the simple extension-reflex. When an ipsilateral stimulus was started during the running of a contralateral extension-reflex the first effect in the curve of the extensor muscle was a phase of relaxation. This again gave place to contraction during the two seconds of the period of double stimulation, and at the point at which the ipsilateral stimulus was withdrawn again the extensor had again attained its former level. Immediately after the withdrawal of the ipsilateral stimulus there was an augmentation of the extensor contraction. This resembled in form the extensor terminal contraction of the simple extension-reflex, but it was much greater in extent (there was no rebound phenomenon in the simple flexion-reflex). It was followed again by the attainment of the ordinary level of extensor immediate contraction, and on cessation of the contralateral stimulus there was another extensor terminal contraction which was less than that in the simple extension-reflex and of course not so great as that obtained on withdrawal of the ipsilateral stimulus in the compound reaction. It looks as if there was here an extensor terminal contraction ("rebound contraction") in response to cessation of a flexion-producing stimulus and during the running of an extension-reflex, although cessation of stimulation in the simple ipsilateral flexion-reflex was followed by no extensor rebound contraction; and as if this was greater than the extensor terminal contraction of the simple extension-reflex (fig. 8).

In a third case (fig. 9) the simple contralateral reaction was a well-sustained extension-reflex. Cessation of stimulation was followed by a sustained "tonic" extensor after-discharge. In the phase of double stimulation of the compound reaction there was complete extensor depression, and the flexor contraction was not so great as in the "pure" flexion-reflex. On withdrawal of the ipsilateral stimulus there occurred a restitution of the extensor contraction; and on subsequent withdrawal of the contralateral stimulus this was maintained as a "tonic" extensor after-discharge.

In another instance (fig. 10) the contralateral reaction, in response to maximum stimulation, opened with a flexor contraction, and later in the period of stimulation gave extensor contraction (4, fig. 35: I notice that in mistake I have described, in the legend of the figure, this reaction as one obtained in the decerebrate preparation, whereas it was obtained in the

low spinal preparation, as I correctly state in the legend of fig. 28). Shortly before this a weaker stimulus had evoked a reaction of pure extension. A weak contralateral stimulus was then applied, and six seconds after its

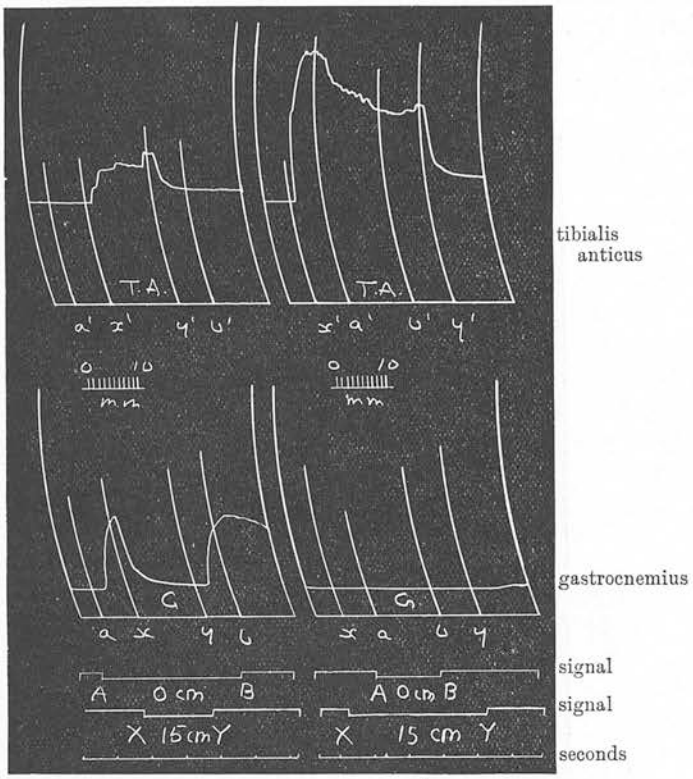


FIG. 9.—Experiment C, cxl., record 258, 6039; 26/11/12.—Low spinal cat, two reactions obtained 4 minutes after division of the spinal cord, there being an interval of 1 minute between the first and second. The stimuli are of constant strength in the two reactions, but their temporal relations are changed.

In reaction *a* the contralateral stimulus is the background. Double stimulation is accompanied by a slight flexor contraction and complete depression of the extensor contraction; on cessation of double stimulation there is an almost complete extensor restitution.

In reaction *b* there is but a slight flexor relaxation during double stimulation, and no extensor contraction. The depression of flexor contraction persists after withdrawal of the interrupting contralateral stimulus, and there is finally a very slight extensor rebound contraction.

Compare here the extents of flexor contraction in the two phases of double stimulation. The reverse phenomena of those of the previous figure are seen. In this case, as it were, the first stimulus to be applied "holds the field."

commencement an ipsilateral stimulus was also given. The contralateral stimulus had evoked no reaction at all, and no extensor contraction appeared in the period of double stimulation. But, on withdrawal of the ipsilateral stimulus (the contralateral stimulus still running), the extensor commenced at once to contract. The contraction was marked, but at once died down

on cessation of the contralateral stimulus, there being then no terminal contraction in either muscle (fig. 10).

In yet another instance—where double stimulation evoked rhythmic contraction of the extensor—the cessation of ipsilateral stimulation was followed by a flexor terminal contraction. Here the flexor contraction during double stimulation had died away, and after withdrawal of the ipsilateral stimulus the extensor contraction suddenly ceased.

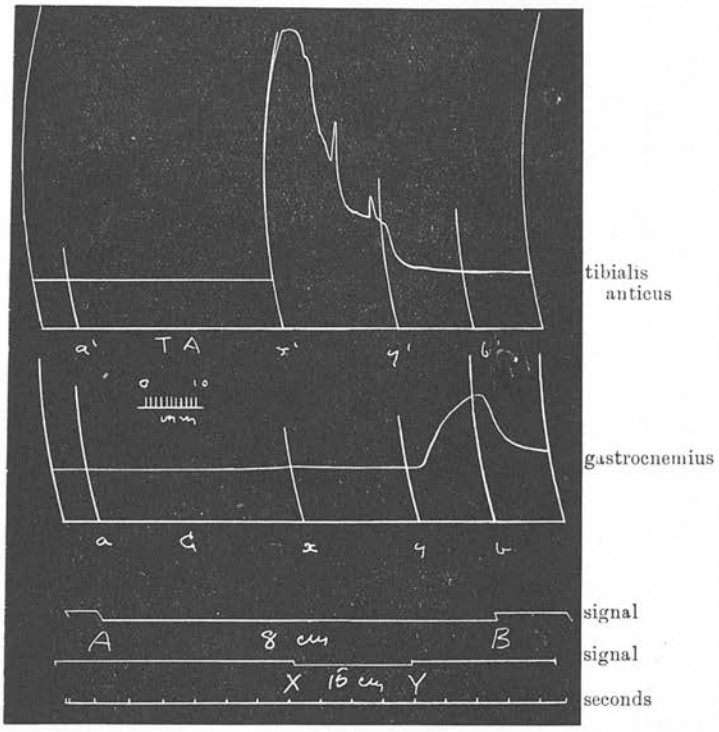


FIG. 10.—Experiment C, xxiv., record 44, 1053; 14/3/11.—Low spinal cat, a record obtained 32 minutes after division of the spinal cord. Here the "background" stimulus is the contralateral. It is run for 6 seconds "pure" and then the ipsilateral stimulus is added. On withdrawal of the latter an extensor contraction appears for the first time in the reaction—demonstrating an effect of extension augmentation as a successive result of double stimulation.

## C. Stimuli of Asynchronous Termination: Ipsilateral Flexion-Reflex left in Action.

In double stimulation records where the ipsilateral stimulus is allowed to continue after cessation of contralateral stimulation, the chief point of interest is the behaviour of the flexor muscle after the withdrawal of the antagonistic reflex. Three possibilities occur: the depression of flexion during the double stimulation may continue after the cessation of the contralateral stimulus, the flexor contraction may "rebound" to the level which it would have had had the ipsilateral stimulus been uninterrupted,

or there may be flexion augmentation to a point above that level. The phenomena can only be observed satisfactorily in those cases in which there is a well-maintained flexor contraction in the ipsilateral flexion-reflex. Where the flexor contraction dies soon during the period of stimulation the after-effect of an intercurrent contralateral stimulus may not be apparent —that is to say, that there may be no flexor augmentation in cases where the flexor contraction, if uninterrupted, would have died away.

In these experiments the method has been to apply an ipsilateral stimulus for a given length of time—say for six or eight seconds—and then at an interval of a minute again to apply it for the same length of time, but to interpose a concurrent contralateral stimulus, which is commenced later than the ipsilateral and ended sooner. The outlines of the two tracings may then be compared, and conclusions drawn from their appearances in the last two seconds (say) of stimulation—when in the compounded curve the contralateral stimulus has been withdrawn. It is advisable to take a third reaction in which the ipsilateral stimulus is again applied pure for the same length of time. If this is similar to the first, it may be assumed that any change in the last portion of the second (intermediate) record is due to the after-effect of the concurrent contralateral stimulus.

In this series of experiments in the low spinal preparation comparative depression of flexion alone was found to follow the withdrawal of the contralateral stimulus.

The contralateral stimulus, when applied during a flexion-reflex, gives relaxation of the flexor contraction. On cessation of the contralateral stimulus the state of flexor relaxation may persist at the same level of relative flexor contraction which obtained (if the relaxation was incomplete) at the end of the period of double stimulation (fig. 4). When the contralateral stimulus is comparatively weak and does not reach its full effect during the period of stimulation used (usually two seconds), the relaxation of the flexor may continue for a short time after the cessation of contralateral stimulation, and then the level reached remains until the end of ipsilateral stimulation. When the period of contralateral stimulation is brief, and is taken early in the period of the flexion-reflex, as time elapses after the withdrawal of the contralateral stimulus the curve of the flexor contraction may at first remain level — although in the corresponding period of a pure flexion-reflex it gradually falls. It then remains level until a point is reached at which the height of contraction is the same as that at the corresponding point in time of the pure reaction—thereafter it falls as in the pure reaction. If the differences in height at different points of the pure reaction and the compounded reaction were plotted as a curve, it would then be found that the relaxation produced during the period of double stimulation was succeeded by a phase of slow reconstitution of the flexor contraction, which finally became nearly complete (fig. 11).

In these cases the amount of flexor relaxation during double stimulation is greater the later in the period of the flexion-reflex the interfering

contralateral stimulus is applied; and the greater also is the amount of relative flexor depression which is left behind at the withdrawal of the contralateral stimulus.

In other cases, although after the withdrawal of the contralateral stimulus the flexor contraction may not again attain to the level which it

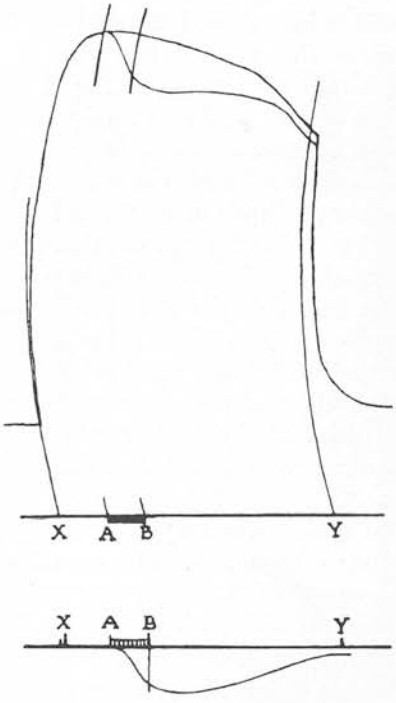


FIG. 11.—This figure is a diagram composed of the outlines of the flexor contractions of the sixth and seventh reactions of fig. 4 (reactions *f* and *g*). Of these the one is a "pure" flexor contraction and the other is a flexor contraction the resultant of this and of a contralateral stimulus applied for about 1 second. The divergence of the two outlines shews a flexor depression during double stimulation (between the ordinates *a* and *b*), and a continuation of this after the termination of double stimulation. On the lower line of the diagram the curve of flexor depression is plotted to a straight line which represents the maintained flexor contraction of a "pure" reaction. Here it is seen that after the end of double stimulation there is a gradual diminution of the relative flexor depression; and that this nearly disappears, but does not quite do so.

would have held if the flexion-reflex had not been interfered with, there may yet be a "rebound" of the flexor contraction (figs. 8, 12, 16).

Thus the flexor may relax during the whole of the period of double stimulation, and this relaxation may continue for as long as 0·75 second after cessation of the contralateral stimulus (fig. 12). Thereafter the flexor contraction augments until it attains a greater degree than that which obtained at the end of double stimulation, but never nearly attains to the degree of maintained contraction which it would have possessed had

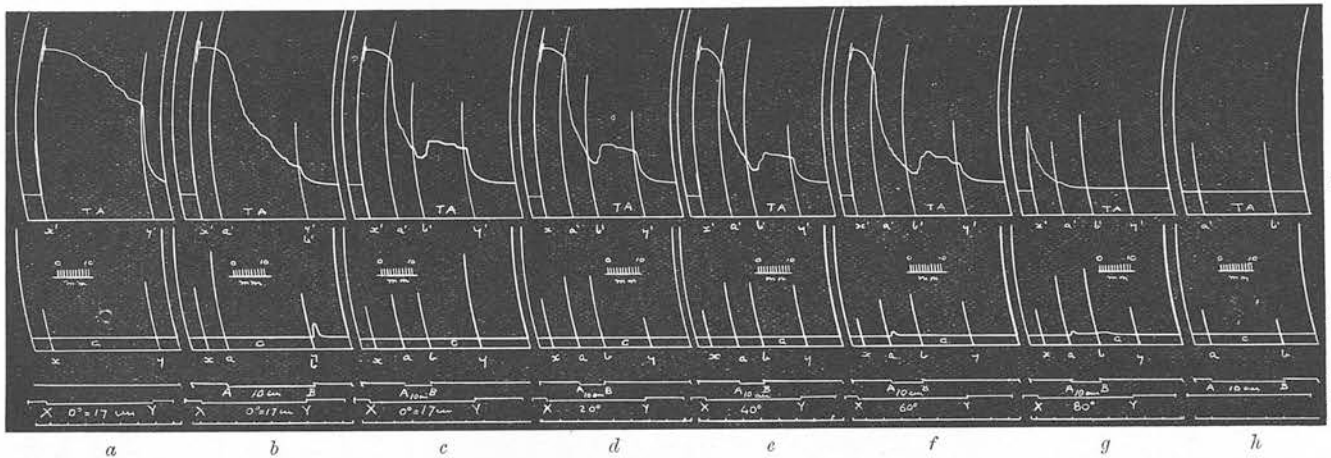


FIG. 12.—Experiment C, xxxii., record 56, 1449 ; 7/4/11.—Low spinal cat, a series of reactions obtained 4 hours and 29 minutes after division of the spinal cord. The reactions are taken at minute intervals, with the exception of the interval between *b* and *c*, which was one of 10 minutes.

The contralateral stimulus used is constant throughout the series and it is subliminal—as is seen in reaction *h*. In reaction *b* the compound stimuli are synchronously terminated, and it will be seen that the cessation of the period of double stimulation is accompanied by an extensor rebound contraction which is present neither in the "pure" contralateral nor in the "pure" ipsilateral reaction (*h* and *a*).

In the series *c* to *g* the contralateral stimulus remains of constant strength, but the ipsilateral "background" stimulus is progressively weakened. During the period of double stimulation the depression of flexor contraction appears to be inversely proportional to the strength of the ipsilateral stimulus. On cessation of double stimulation a certain amount of restitution of flexor contraction occurs. This seems in extent to be directly proportional to the strength of the ipsilateral stimulus. In reaction *f* a slight extensor contraction appears during the period of double stimulation, and this is better marked in reaction *g*. Nevertheless, there is no extensor contraction when the contralateral stimulus is applied "pure"—reaction *h*.

[From the same experiment as figs. 1, 2, 6, and 8.]

there been no interposed antagonistic stimulus. This level is then held until the end of the period of ipsilateral stimulation. The augmentation is sometimes a rapid movement, but sometimes a slow one.

In one instance of this nature (fig. 12) it was found that there was a sudden augmentation of the rate of flexor relaxation on cessation of the contralateral stimulus. In this case the contralateral reaction was one followed by an extensor terminal contraction after excitation; and the case is of interest in that almost certainly this augmentation of relaxation is strictly comparable to the "extensor rebound relaxation after inhibition" described in a previous paper of this series (3), and therefore extends the observation of the phenomenon to the flexor muscle and to the low spinal preparation.

When the time relations of the two stimuli are kept constant in a series of reactions, and when the contralateral stimulus is kept of constant strength but the ipsilateral progressively decreased in value, it may be found that the extent of the restitution of flexor contraction after withdrawal of the contralateral stimulus progressively decreases with decrease of the value of the "background" flexion-reflex (fig. 12). Restitution seems to be greater also the earlier in the period of the flexion-reflex the contralateral stimulus falls (fig. 8).

## V. Low Spinal Preparation—De-afferented Condition.

In the de-afferented condition of the low spinal preparation the two antagonistic stimuli have been combined in different temporal arrangements, and the resultant reactions confirm those obtained in the normal condition.

Of the immediate effects of the double combination, an augmentation of the extent of extensor contraction has been observed. In this instance the extensor contraction during the phase of double stimulation was much greater than in the "pure" extension-reflex. At the same time there was an extensor terminal contraction after excitation in the "pure" extension-reflex, and this also was augmented in the compound reaction. When a strength of contralateral stimulation which when given "pure" was ineffective was applied—and when the effect of double stimulation was not that of extension augmentation—on withdrawal of the ipsilateral stimulus there might be a sudden augmentation of the extensor contraction during the running of the remaining portion of the period of contralateral stimulation.

In other cases it has been observed that, with a sufficiently strong ipsilateral stimulus, double stimulation results (as in the normal condition) in a depression of the extensor contraction of the extension-reflex. When both stimuli are taken off at the same time there may be an extensor terminal contraction which is markedly greater than the extensor terminal contraction after excitation of the pure extension-reflex (fig. 13). (Here there was no terminal rebound contraction on cessation of stimulation in the "pure" ipsilateral flexion-reflex.)

Where an ipsilateral flexion-producing stimulus is applied for a given length of time and during its application a contralateral stimulus is given and taken off again, the phenomena are very similar to those obtained in the normal condition.

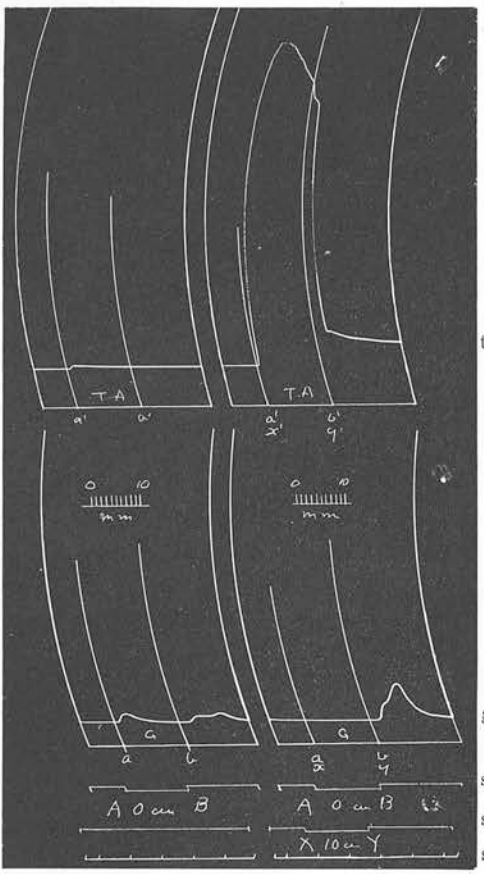


FIG. 13.—Experiment C, 1., record 88, 2234; 19/6/11.—De-afferented condition of low spinal preparation—cat; two reactions obtained 1 hour and 20 minutes after division of the spinal cord (and 7 hours and 41 minutes after decerebration).

Reaction *a* demonstrates a "pure" extension-reflex in which the extensor contraction is slight, and in which there is a slight extensor rebound contraction on cessation of stimulation. In reaction *b* this stimulus is synchronously compounded with an ipsilateral. Flexor contraction accompanied by abolition of extensor contraction occurs during double stimulation. On termination of this period there is an extensor rebound contraction which is much greater in extent than in *a*. (A "pure" ipsilateral reaction was not followed by an extensor rebound contraction.)

[From the same experiment as figs. 14 and 15.]

During the phase of double stimulation there is a state of relative relaxation of the flexor. The extent of this varies, and depends upon the relative strengths of the two antagonised stimuli. Where the strength of

the ipsilateral stimulus is relatively great the relaxation of the flexor is relatively small; and where relatively small the relaxation of the flexor is relatively great. In the latter circumstances extensor contraction may

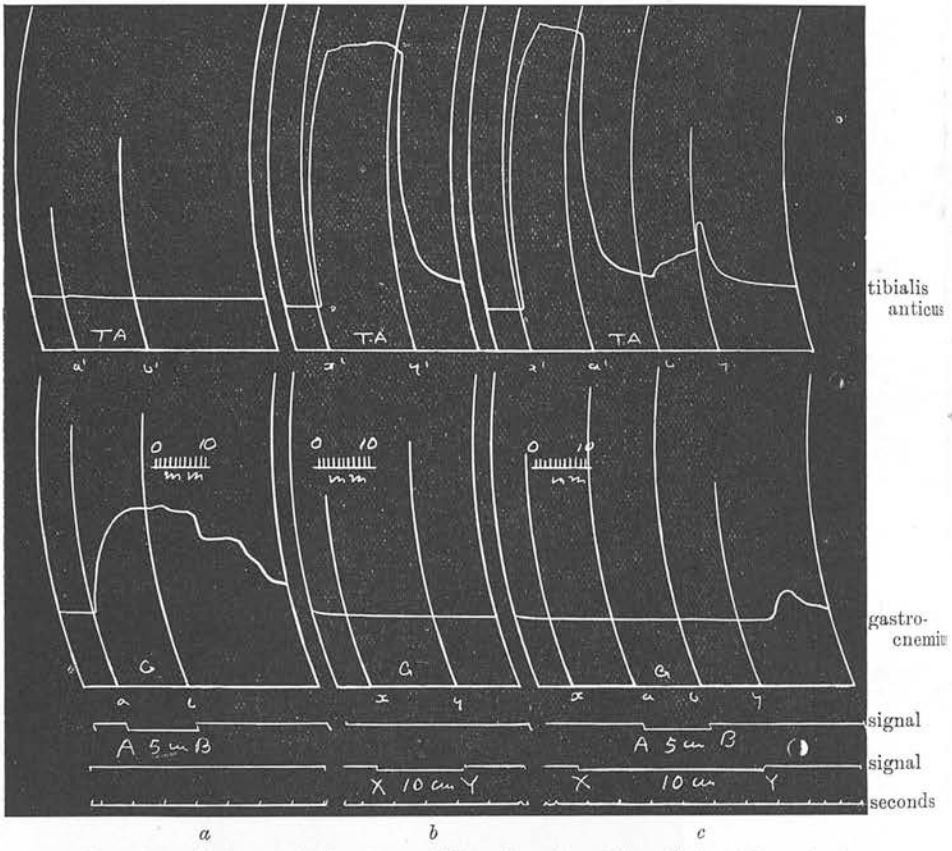


FIG. 14.—Experiment C, l., record 87, 2204; 19/6/11.—De-afferented condition of low spinal preparation—cat; three reactions obtained 3 minutes after division of the spinal cord (and 6 hours and 24 minutes after decerebration). Minute intervals elapse between the reactions.

Reactions *a* and *b* are "pure" contralateral and ipsilateral reflexes. Reaction *c* is compound of the two. The ipsilateral is the "background" stimulus. Depression of flexor contraction occurs during double stimulation, but is unaccompanied by extensor contraction. On cessation of double stimulation there is a partial restitution of flexor contraction, and on cessation of ipsilateral stimulation there is first a flexor rebound contraction and then an extensor—neither of these phenomena occurring in the "pure" reactions, although it must be noted that in reaction *b* the ipsilateral stimulus is applied for a shorter time than in reaction *c*. Note here the extensor "after-discharge" in reaction *a*.

[From the same experiment as figs. 13 and 15.]

appear during the phase of double stimulation; but this will not appear when the strength of ipsilateral stimulation is relatively great.

After withdrawal of the contralateral stimulus and when the flexion-reflex is still in action there may be a partial restitution of flexor contraction. But in these experiments this has never been to the level of

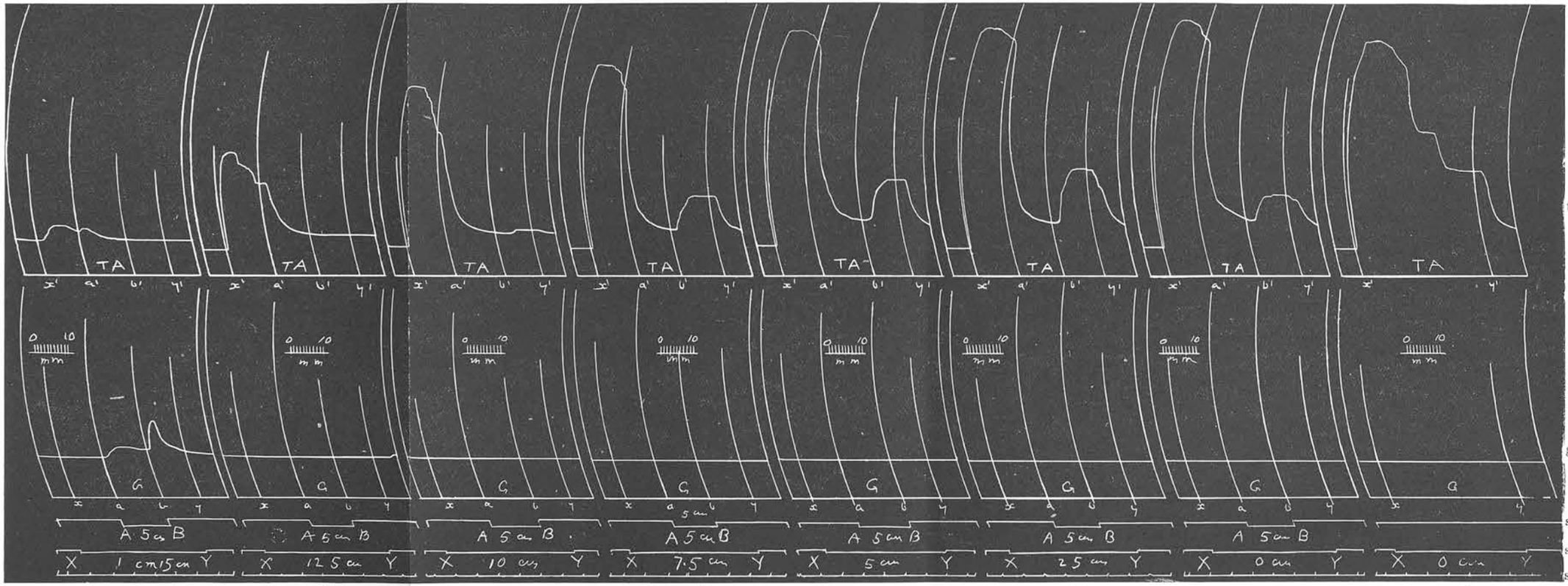


FIG. 15.—Experiment C, l., record 87, 2209; 19/6/11.—De-afferented condition of low spinal preparation—cat; a series of reactions obtained 8 minutes after division of the spinal cord (6 hours and 29 minutes after decerebration). Intervals of 1 minute each intervene between successive reactions. The interrupting contralateral stimulus is constant in strength throughout the series; the background ipsilateral stimulus is increased in strength in successive reactions. Reaction *h* is a "pure" ipsilateral flexion-reflex.

In reaction *a*—where the "background" is weak—there is a certain amount of extensor contraction during double stimulation, and in the commencement of that period there seems to be a slight augmentation of the flexor contraction. Cessation of double stimulation is seen to be followed by an extensor rebound contraction. This was present in the "pure" extension-reflex (see reaction *a* of fig. 3 in the paper of this series immediately preceding the present one).

In the succeeding reactions no extensor contraction occurs. The flexor relaxation during double stimulation appears to decrease in extent with increase in the value of the background stimulus. On cessation of the contralateral stimulus there is no flexor restitution of contraction in reaction *b*, but this appears in *c*, and thereafter becomes greater with increase in the value of the background stimulus. In reaction *b* a slight extensor rebound contraction occurs on cessation of the ipsilateral stimulus.

[From the same experiment as figs. 13 and 14.]

contraction which would have obtained had there been no interruption. In one instance, on withdrawal of the ipsilateral stimulus, there was a flexor terminal contraction, followed later by an extensor terminal contraction. In the pure flexion-reflex neither of these phenomena occurred (fig. 14).

In one instance a series of compounded reactions in which the "background" stimulus of ipsilateral flexion was progressively increased in value but in which the interrupting contralateral stimulus was kept constant was obtained. Here it was observed that where the ipsilateral stimulus was very weak the commencement of the period of double stimulation appeared to be accompanied by a slight augmentation of the small flexor contraction. Synchronously there was a well-marked extensor contraction, and the flexor soon completely relaxed. The extensor contraction remained during the period of double stimulation, and at the withdrawal of the contralateral stimulus there was a marked extensor terminal contraction. There was no restitution of flexor contraction during the remaining period of ipsilateral stimulation. On using greater strengths of ipsilateral stimulation there was then found not to be any extensor contraction. With a strength of ipsilateral stimulation greater than that just described there was a nearly complete relaxation of the flexor during the period of double stimulation. But there was no restitution of the flexor contraction when the contralateral stimulus was withdrawn. As the strength of ipsilateral stimulation was increased the relaxation during the period of double stimulation decreased in extent, and restitution appeared and became ever greater the greater the strength of ipsilateral stimulation (fig. 15).

## VI. Low Spinal Preparation—Abnormal Reactions.

In the low spinal preparation the ipsilateral extension-reflex is a reaction of great rarity; but the abnormal contralateral flexion-reflex is not uncommon—at any rate as studied in the movements of the ankle which are evoked in response to stimulation of the saphenous nerve. This reaction has in these experiments been compounded with the normal ipsilateral flexion-reflex both in the normal and in the de-afferented condition.

When an ipsilateral and a contralateral flexion-reflex are synchronously compounded it might be supposed that the resultant reaction would be flexion of greater extent than either. Although this may occur, very often the reverse takes place.

In one experiment where the extents of the ipsilateral and contralateral flexion-reflexes were small, it was found that when both were applied together there was a slight augmentation of flexion during double stimulation, so that the resultant contraction was greater than that of either pure reaction. If, however, the ipsilateral flexion was first put in action and then, later in the period of stimulation, the contralateral flexion was added, the result was a slight depression of flexion. When the contralateral

flexion was first applied and taken off (after two seconds) at the same moment that an ipsilateral stimulus was commenced (successive compounding), the ipsilateral flexion-reflex was found to be markedly depressed in comparison with the pure reaction obtained with the same strength of stimulus. These reactions were all obtained when the strength of ipsilateral stimulation was small. When the ipsilateral stimulus was a strong one similar effects were obtained. When the ipsilateral stimulus immediately followed upon cessation of the contralateral (compounding in temporal succession), it was again found that there was depression of ipsilateral flexion (fig. 16). When the contralateral stimulus was applied during the ipsilateral and after its commencement, it was then found that there was a well-marked relaxation of flexor contraction, just as if the contralateral reaction had been a normal extension-reflex (fig. 16). When the contralateral stimulus was then taken off again during the continuance of the ipsilateral flexion-reflex, it was found that there was a restitution of the extent of flexor contraction. But the reëstablishment of flexor contraction was not complete—that is to say, it did not bring the level of the curve up to that which would have obtained had the ipsilateral flexion-reflex been uninterrupted.

In this experiment the "double step" combination of the two stimuli gave reactions of great interest. In this form of combination of two stimuli in time one stimulus is first applied, and during its application the second is commenced. For a short time both stimuli are allowed to run together, and then the first is taken off. The second then runs alone and finally itself is stopped (fig. 16).

When the contralateral stimulus was first applied it was found (both when the ipsilateral stimulus was a strong one and when it was weak) that, when the ipsilateral stimulus was added to it after one second had passed, there was an augmentation of flexion. This was, however, not to so great a level as when the ipsilateral stimulus was applied alone. When, then, the contralateral stimulus was taken off and the ipsilateral alone was in action, the flexor contraction augmented. Although its phase of increasing contraction was a slow one, yet eventually it terminated at a level only slightly less than that which a pure ipsilateral reaction would have had at the same length of time after its commencement.

If the stimuli were taken in the reverse order, similar appearances were obtained (fig. 16). Here the commencement of contralateral stimulation during the period of ipsilateral stimulation was accompanied by relaxation of the flexor contraction. If then the ipsilateral stimulus was taken off, the flexor still further relaxed. But it did not relax down to so low a level as would have obtained in the flexor contraction of the pure contralateral flexion-reflex.

In another experiment some of these phenomena were observed within the first eleven minutes after division of the spinal cord (the preparation had been a decerebrate one). Here, when the contralateral stimulus was

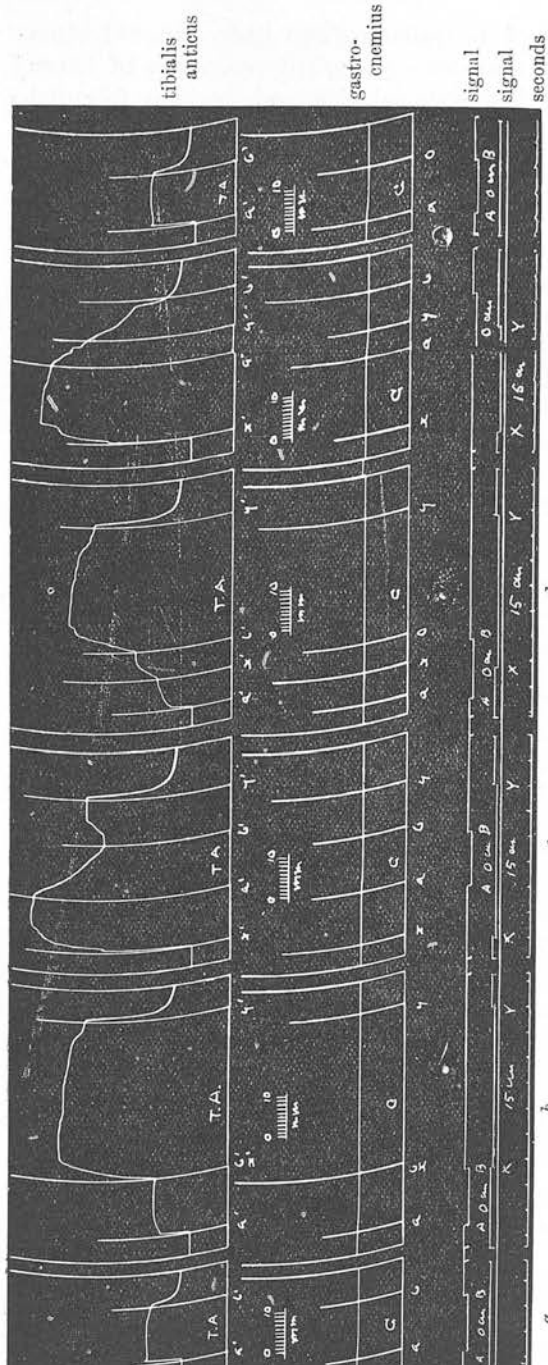


FIG. 16.—Experiment C, xxix., record 53, 1353 ; 30/3/11.—Low spinal cat, a series of compound reactions obtained 6 hours and 37 minutes after division of the spinal cord. The stimuli are arranged in different temporal relationships, and the contralateral reaction is one of abnormal flexion.

Reaction *a* is a "pure" contralateral one, and demonstrates an abnormal crossed flexion-reflex. In reaction *b* this is made immediately to precede an ipsilateral reaction—there being successive compounding but not immediate compounding of the two reactions. The ipsilateral flexion-reflex is depressed—as may be seen on comparison with the first part of the following reaction, where the ipsilateral flexion is "pure." In reaction *c* the contralateral stimulus interrupts the ipsilateral, which here is the "background" stimulus of a compound reaction. There is seen to be flexor relaxation during double stimulation, and not flexor augmentation. A certain amount of flexor restitution of contraction follows the withdrawal of the contralateral stimulus. In reaction *d* the stimuli are in "step" arrangement—first contralateral, then both, then ipsilateral alone. During double stimulation there is augmentation of flexion from the level of the contralateral contraction, but not up to the level of the "pure" ipsilateral flexion. Note that the level of flexor contraction attained here is less than that which obtains during double stimulation in the preceding reaction. After cessation of the contralateral stimulus there is a further augmentation of flexor contraction, but the level attained is not so great as that attained at the same point in a "pure" ipsilateral reaction. In reaction *e* the stimuli are again in "step" arrangement, but in the reverse order. Here double stimulation is accompanied by flexor relaxation, and cessation of the contralateral stimulus is followed by a still further relaxation of flexor contraction, while the contralateral stimulus is continued. The level of flexor contraction at the end of contralateral stimulation is, however, considerably greater than that which obtains in the "pure" contralateral reaction. [Note that ordinates *b*, *b'* have accidentally been drawn about 2 mm. (reduced scale) too far to the right of the tracing.] Reaction *f* is again a "pure" contralateral flexion-reflex.

[From the same experiment as fig. 4.]

applied after the commencement of the ipsilateral and again removed while the ipsilateral was still in action, there was a marked relaxation of flexor contraction during the period of double stimulation, and this was followed by as marked a reconstitution of flexor contraction—although that was not complete.

In one experiment the compounding of the abnormal crossed flexion with the ordinary ipsilateral flexion has been examined in the de-afferented condition of the low spinal preparation. At this stage in the experiment the contralateral stimulus evoked a reaction characterised by flexor contraction during stimulation, and by an extensor terminal contraction (rebound). Ten minutes before there had been extensor contraction during stimulation. Here, when the contralateral stimulus was commenced and stopped during the period of application of the ipsilateral, there was a marked relaxation of flexor contraction during double stimulation. This was followed by partial restitution when the contralateral stimulus was taken off. When both stimuli were commenced at the same time the extent of flexor contraction at first was slightly greater than that which would have been present in a pure ipsilateral flexion-reflex, and was present in a reaction taken after an interval of one minute. The curve of flexor contraction, however, then commenced to fall, and did so more rapidly, so that at the end of the two seconds of double stimulation the level was slightly lower than that which obtained at the end of the second second of pure ipsilateral stimulation. The cessation of the two stimuli was followed by an extensor terminal contraction which was of about the same extent as in the pure contralateral reaction. In this same experiment, seven minutes earlier, when the contralateral reaction had been one of extension, the similar compounding of the two stimuli (of the same strength as in the case described above) was followed by a marked augmentation of an extensor terminal contraction which was present in the extension-reflex as an extensor terminal contraction after excitation.

### VII. High Spinal ("Decapitate") Preparation—Immediate Effects.

In the high-spinal preparation phenomena similar to those of the low-spinal preparation have been seen.

The flexor muscle during double stimulation contracts to a less degree than in a simple flexion-reflex evoked by the same strength of ipsilateral stimulation (fig. 19) When strong contralateral stimuli are compounded with weak ipsilateral there may be almost no flexor contraction during double stimulation; where the ipsilateral stimulus is relatively strong, the flexor contraction may be only slightly smaller than that in the "pure" flexion-reflex.

In the case of the extensor muscle (figs. 17, 18, 19) the phenomenon of extensor augmentation during double stimulation has rarely been observed (fig. 20) in the series of experiments in decapitate preparations. The

extensor contraction has been found to be smaller than in a pure extension-reflex evoked with the strength of contralateral stimulation compounded with the ipsilateral. But in these experiments the two antagonistic stimuli were not applied and again taken off at the same times, and the immediate effects of double stimulation are described from experiments in which the one stimulus was applied during the running of the other. The extensor contracts to an extent intermediate between that of the pure extension-reflex and zero, and the relative extent of this intermediate contraction depends upon the relative values of the two antagonistic stimuli com-

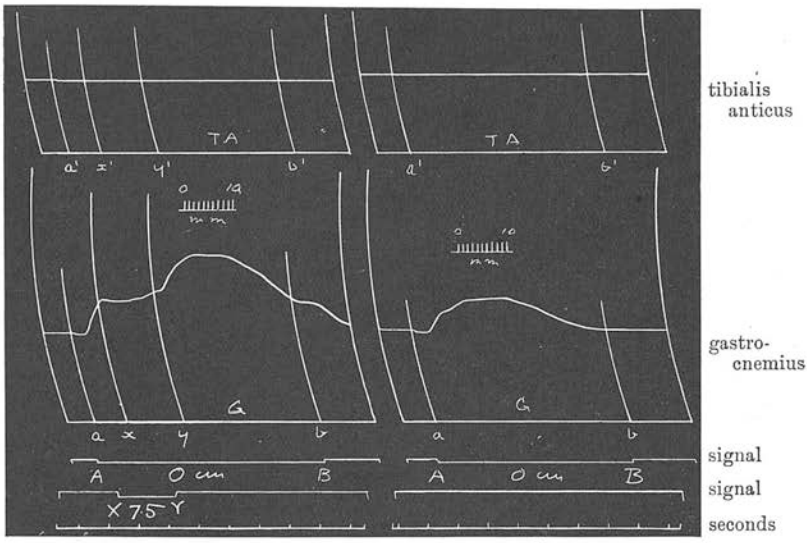


FIG. 17.—Experiment C, xli., record 72, 1772; 18/5/11.—High spinal (decapitate) cat, two reactions obtained 26 minutes after decapitation (4 hours and 1 minute after decerebration). An interval of 2 minutes elapsed between them. Reaction *a* shews the effect of interrupting an extension background with an ipsilateral stimulus. During double stimulation there is a slight depression of extensor contraction. Cessation of the ipsilateral stimulus is followed by an augmentation of extensor contraction greater than that in the "pure" contralateral reaction—reaction *b*. [From the same experiment as figs. 19 and 20.]

pounded. Where the ipsilateral flexion-producing stimulus is relatively strong the extensor contraction may be almost zero; where it is relatively weak the extensor contraction may be very nearly of the same extent as in the pure extension-reflex evoked by the same strength of contralateral stimulation.

Thus in these experiments the immediate effects of the synchronous compounding of two antagonistic stimuli have taken the form of "algebraic summation." The two muscles have simultaneously contracted, but the contraction of neither has been as great as in a pure reflex evoked by the same strength of stimulus. Compared with the extent of contraction in a simple reflex, the flexor contraction has been found to be least reduced

—and the extensor most—when the ipsilateral flexion-producing stimulus has been of greatest relative strength; and the flexor contraction has been most reduced—and the extensor least—when the relative strength of the contralateral extension-producing stimulus has been greatest.

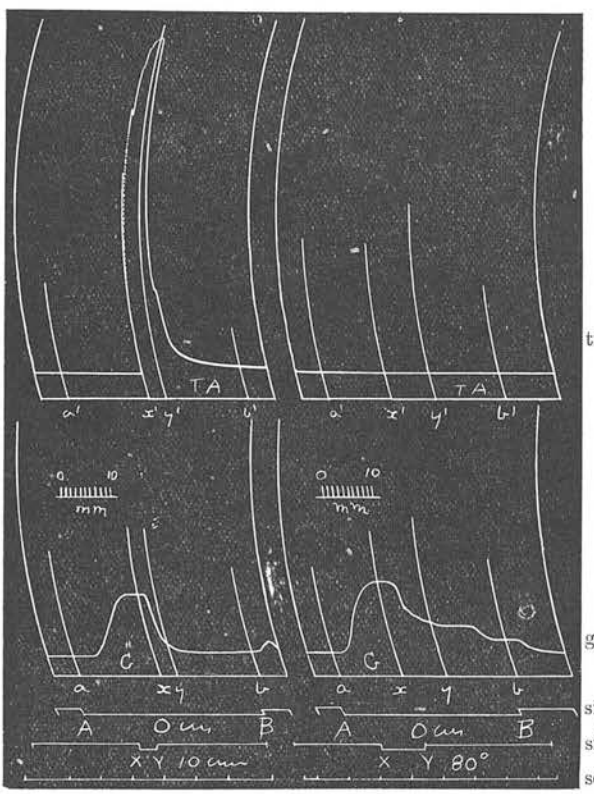


FIG. 18.—Experiment C, xlv., record 76, 1905; 25/5/11.—High spinal (decapitate) cat, two reactions obtained 5 hours and 45 minutes after decapitation. There is an interval of a minute between them. In reaction *a* a strong ipsilateral stimulus is compounded against a background of extension. During double stimulation there is almost complete extensor relaxation, although the period of the ipsilateral stimulus is short. Cessation of the ipsilateral stimulus is followed by a complete depression of extensor contraction, but on withdrawal of the contralateral stimulus there is a slight extensor rebound contraction. In reaction *b* the ipsilateral stimulus is very weak, and the same strength of contralateral stimulation is used as the background. Here there is an extensor relaxation during double stimulation which is much less than before. During the third phase of the reaction the extensor remains in reduced contraction—there is not complete depression as in *a*. No extensor rebound contraction occurs here on cessation of the contralateral stimulus.

## VIII. HIGH SPINAL ("DECAPITATE") PREPARATION—SUCCESSIVE EFFECTS.

### A. Stimuli of Synchronous Termination.

In these experiments the two stimuli were never stopped synchronously, and therefore no data with regard to the terminal effects of double stimulation exist.

### B. Stimuli of Asynchronous Termination: Contralateral Extension-Reflex left in Action.

When the contralateral stimulus is first applied and the ipsilateral flexion-producing stimulus is commenced during its application and terminated before its cessation, the state of the centres passes from that

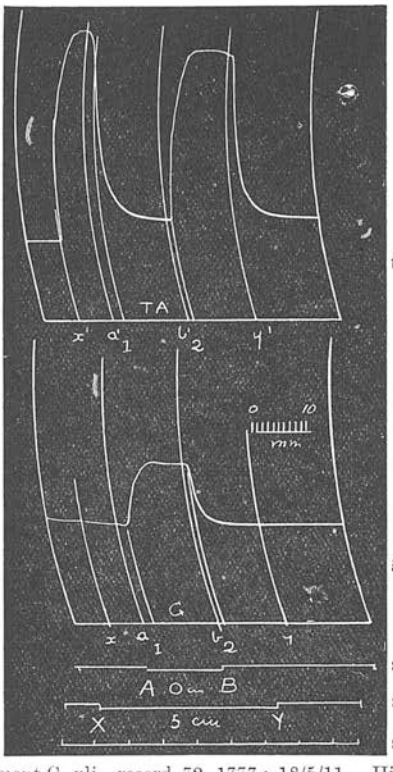


FIG. 19.—Experiment C, xli., record 72, 1777; 18/5/11.—High spinal (decapitate) cat, a reaction obtained 32 minutes after decapitation (4 hours and 7 minutes after decerebration). Here a contralateral stimulus interrupts a background of ipsilateral flexion. During double stimulation there is a marked flexor relaxation, and a reciprocal extensor contraction. Withdrawal of the contralateral stimulus gives a nearly complete restitution of flexor contraction during the remaining portion of the period of the ipsilateral stimulus. The numbered ordinates 1 and 2 demonstrate the time relationships of the reciprocal movements of contraction and relaxation in the two muscles. It is seen that relaxation precedes contraction by an appreciable interval of time.

[From the same experiment as figs. 17 and 20.]

which obtains during the double stimulation to the state of "rest" in two steps. The first of these is that in which the contralateral stimulus is still being applied alone, and the second is the state immediately after cessation of that stimulus. As in these experiments with decapitate preparations there were no rebound phenomena, the results give no information with regard to the happenings after the withdrawal of the final stimulus.

But in these experiments data concerning the effects of withdrawal of the ipsilateral stimulus upon the response to the still continuing contralateral stimulus have been obtained.

It sometimes occurs that a marked augmentation of the contralateral effect—that is to say, of the extensor contraction—may follow the withdrawal of the ipsilateral stimulus (fig. 17). This may be shewn by the attainment of a state of extensor contraction greater than that obtained in the simple extension-reflex evoked with the same strength of contralateral stimulation. Or there may be no extensor contraction in response to contralateral stimulation in the period of stimulation before commencement of the ipsilateral stimulus. Contraction may then appear during the period of double stimulation, and may then markedly augment on withdrawal of the ipsilateral stimulus.

In these experiments this effect has been found to occur when the strength of ipsilateral stimulation is very weak. If it be increased in strength there is a greater depression of the extensor contraction during double stimulation, and at the withdrawal of the ipsilateral stimulus there is an increase of the extent of extensor contraction—but perhaps not to the level which would have been obtained in a simple contralateral extension-reflex evoked with the same strength of stimulus.

Where the strength of ipsilateral stimulation is still greater there may be no recovery of the extensor contraction at the withdrawal of the ipsilateral stimulus (fig. 18); and when it is very great there may be complete relaxation of the extensor contraction during double stimulation, and again no recovery. In one instance there was an extensor terminal contraction on cessation of the contralateral stimulus, although this was not present in the simple extension-reflex (fig. 18).

### C. Stimuli of Asynchronous Termination: Ipsilateral Flexion-Reflex left in Action.

The phenomena observed when the ipsilateral stimulation was first applied and during its application the contralateral was started and stopped have been the same as in the low spinal preparation. In one experiment the relaxation of the flexor contraction during double stimulation (in response to a strong contralateral stimulus) was very nearly complete—and yet there was a very nearly complete restitution on withdrawing the contralateral stimulus (fig. 19).

### D. Double Stimulation in "Step" Arrangement.

In this form of temporal arrangement of two antagonistic stimuli one is first applied and then, while the first is running, the second is commenced; the first is then stopped while the second is allowed for a time to continue.

In the decapitate preparation the results obtained have resembled those found in the low spinal preparation.

When the first of the two antagonistic stimuli is the ipsilateral (fig. 20), the extensor contraction during the period of double stimulation has been found to be greater than in a pure extension-reflex evoked at the same strength of contralateral stimulation. On withdrawal of the ipsilateral

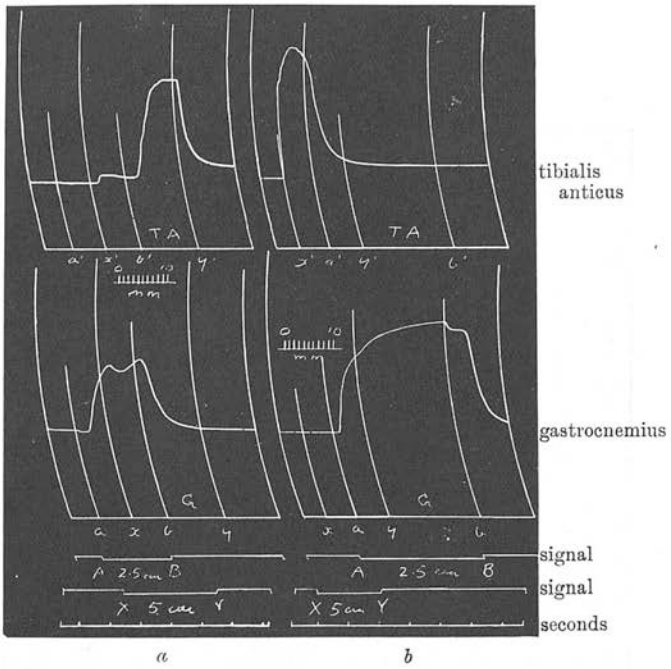


FIG. 20.—Experiment C, xli., record 72, 1883; 18/5/11.—High spinal (decapitate) cat, two reactions obtained 38 minutes after decapitation (5 hours and 13 minutes after decerebration). An interval of 1 minute elapses between them. The stimuli are arranged in "step" formation. In reaction *a* the contralateral stimulus is first applied. During double stimulation a slight extensor depression of contraction and a slight flexor contraction occur. On withdrawal of the contralateral stimulus there is an augmentation of the flexor contraction and a further depression of extensor contraction. The latency of the flexor augmentation of contraction is great, and its extent is smaller than in the "pure" ipsilateral reaction—as may be seen on comparison with the flexor contraction in the first part of reaction *b*. In reaction *b* the stimuli are arranged in the reverse order. Here double stimulation is accompanied by flexor relaxation and extensor contraction. The extensor contraction is of shorter latency than in the "pure" reaction (first part of reaction *a*), and is of slightly greater extent. Withdrawal of the ipsilateral stimulus is followed by a very slight—but distinct—extensor augmentation of contraction.

[From the same experiment as figs. 17 and 19.]

stimulus (the contralateral then running alone) there may be an augmentation of the extensor contraction.

When the first stimulus to be applied is the contralateral, there may be a diminution of the extensor contraction during the phase of double stimulation, and at the same time the flexor contraction may be less—perhaps much less—than in the simple flexion-reflex of the same strength of ipsilateral stimulation. On withdrawal of the contralateral stimulus the flexor contraction augments. The extent of this contraction was in

one instance very nearly to the level which would have obtained in a simple ipsilateral reaction of the same strength and after the same duration of stimulation. In another instance it was very much less.

IX. High Spinal ("Decapitate") Preparation—Abnormal Reactions.

In one experiment in which a decapitate preparation was used the contralateral reaction was that of abnormal flexion. Here it was found

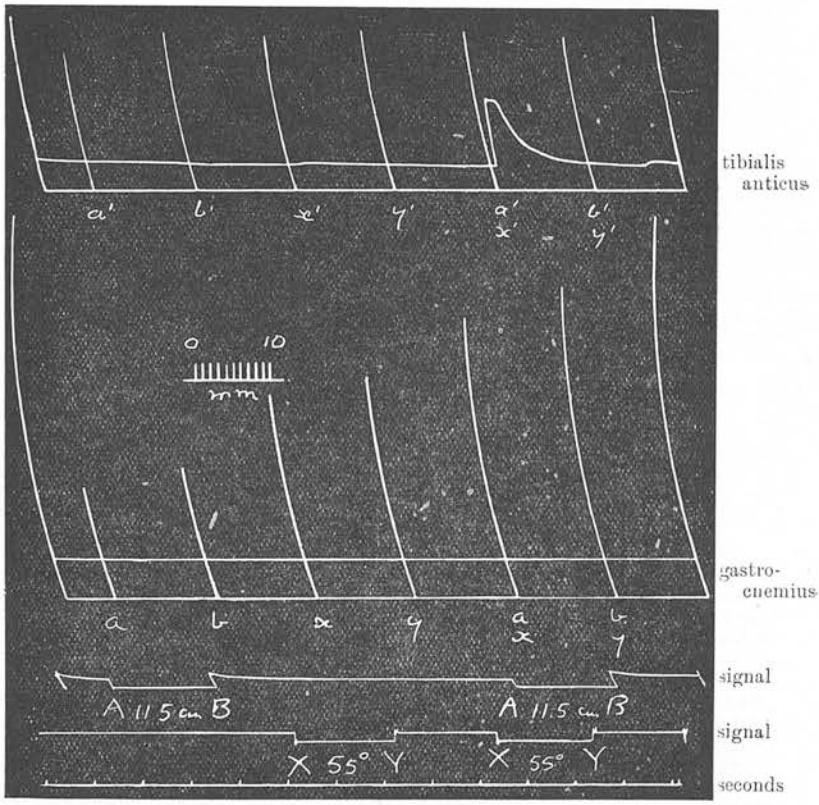


Fig. 21.—Experiment C, xlii., record 73, 1806; 20/5/11.—High spinal (decapitate) cat, a compound reaction obtained 6 hours and 2 minutes after decapitation. In this experiment the contralateral reaction was one of abnormal crossed flexion (see fig. 29 of paper xi. of this series—from the same experiment). Here a subliminal contralateral stimulus is first applied; then after an interval of about 2 seconds an almost subliminal ipsilateral stimulus is applied; finally, after another 2 seconds, the two are applied synchronously and a marked flexor contraction results. This demonstrates a summation of two subliminal ipsilateral and contralateral stimuli where the crossed and the uncrossed reactions are both flexion-reflexes.

that when subliminal ipsilateral and contralateral stimuli were given simultaneously (starting at the same moment) there was evoked a distinct reaction of flexion (fig. 21). Later in this same experiment—when the contralateral stimulus evoked no reaction, and when the ipsilateral stimulus

was first applied and the contralateral commenced during this stimulation and also taken off again before its termination—there resulted a partial flexor relaxation during the phase of double stimulation. On termination of the contralateral stimulus the flexor contraction was in part reconstituted —but not nearly to the level of contraction which would have obtained had the ipsilateral stimulus been uninterrupted.

## X. Conclusions.

In the recent spinal preparations when two antagonistic stimuli are compounded together there is usually conditioned a reflex state in which the state of contraction of each of the two antagonistic muscles (as examined at the ankle) is less than in the respective uncompounded reactions but greater than the zero of the state of "rest."

When this occurs there is an algebraic summation of the two antagonised acts in Sherrington's sense. That is, in each half-centre—as estimated by the state of its respective muscle—there is an algebraic compounding of the activation conditioned by one stimulus and of the inhibition conditioned by the antagonistic stimulus.

The extent of the contraction in either muscle varies with the relative strengths of the two compounded stimuli—as Sherrington has pointed out in the decapitate preparation. When one stimulus is relatively much stronger than the other, then the activation conditioned by it in one half-centre by much outweighs the inhibition conditioned in that half-centre by the other stimulus, and the muscle which is subservient to that half-centre contracts little less strongly than in the "pure" reflex. At the same time the inhibition conditioned by the stronger stimulus in the other half-centre by much outweighs the activation conditioned by the weaker stimulus, and that muscle contracts much less than in the other "pure" reflex compounded in the reaction of double stimulation.

Where either of the two antagonistic stimuli is very much greater than the other, the contraction of the muscle which it inhibits may be completely suppressed. In these circumstances it is interesting to note that the contraction of the muscle which it activates may still be less than in the "pure" reflex obtained at the same strength of the stimulus which activates it. That is to say, that a comparatively weak stimulus, which in the phase of double stimulation of a compound reaction is unable to condition contraction of the muscle it activates, may yet evidence itself by partial inhibition of the other muscle of the antagonistic pair.

The phenomena in the phase of double stimulation of a compound reaction, as stated above, vary with the relative strengths of the two compounded stimuli. In successive compound reactions the relative values of the stimuli may be graded, and there is then grading of the respective reflex muscular contractions. At one end of such a series there may be complete suppression of the contraction of one antagonist, and slight

suppression only of that of the other. At the other end of the series there may be slight suppression of the contraction of the former, and complete suppression of that of the latter. While between the two extremes various degrees of algebraic summation may be observed.

The phenomena vary also with the time relations. Even within the period of double stimulation there is usually a variation as time advances. At the beginning of such a phase—let us say, one in which the two stimuli run together for a period of two or four seconds—flexion activity usually more preponderates over extension activity than at the end of it. In a graded series of compound reactions in which the value of the extension-producing stimulus is relatively increased in succeeding reactions, there may at first be complete suppression of extensor contraction during double stimulation. As the strength of the extension-producing stimulus is then relatively increased, extensor contraction may appear. But when it first does so, its appearance is late in the period of double stimulation—the latency of extensor contraction is great, and its extent is small. With greater increase of the relative strength of the extension-producing stimulus the latency of extensor contraction decreases, and its extent increases.

Another temporal relationship which may be examined is that in which one stimulus is applied before the other, so that the effect of double stimulation may be examined as that period falls at different times after the commencement of one of the antagonistic reflexes or of the other.

When the flexion-reflex is first applied it is found that the flexor depression and extensor contraction during double stimulation are (within limits) greater the later in the period of the flexion-reflex the phase of double stimulation falls. A maximum effect is obtained when a certain interval of time elapses between the commencement of the flexion-reflex and that of the antagonistic stimulus. As the flexor contraction soon "fatigues," this is best seen in the extensor contraction during double stimulation. When the phase of double stimulation is applied later than the optimum interval, the extensor contraction of double stimulation again becomes less. As the extension-reflex is usually easily "fatigued" in the spinal preparations, no very satisfactory results have been obtained when the extension-reflex is made to precede the phase of double stimulation. It has appeared, however, that the flexion effect in the compound phase was greater the later it fell after the commencement of the extension-producing stimulus. But it is great also when the two stimuli are commenced synchronously. Then perhaps there is a summation of the flexion-reflex and the preliminary flexion factor in the extension-reflex which is often present, and when absent may be only masked. If the period of double stimulation then falls a little later, there is a relative depression of flexion, and then still later periods give greater flexion effects again. Whether this is the invariable effect it is not possible from these experiments to say.

A curious demonstration of these temporal relations is given when, in

two successive compound reactions, the same strengths of antagonistic stimuli are used, but when in one case one is started before the other, while in the other case the second stimulus is started before the first—in either case the period of double stimulation falling at the same point of time after the commencements of the respective first stimuli. It is then found that the algebraic summations in the two phases of double stimulation are not the same, although the same strengths of stimuli are used in each case. Thus if flexion be first applied, the extensor contraction during double stimulation may be less and the flexor contraction may be greater than when the extension-reflex is first applied. Sometimes the opposite effects are seen. It looks as if sometimes the first stimulus "holds the field," and as if at other times it "fatigues," so that the second stimulus has a greater relative value.

An interesting point in connexion with these experiments is the extensor augmentation which is sometimes seen during double stimulation. This has been observed in the low spinal preparation. Sometimes the extensor contraction is actually greater than in the "simple" extension-reflex evoked at the same strength of stimulus. In these cases the extent of the extensor contraction increases, up to a certain point, with relative decrease of the strength of flexion-producing stimulation in the compound reaction. Thereafter, as the flexion stimulus is still further decreased, there may occur a decrease in the extent of the extensor augmentation. This phenomenon perhaps demonstrates the extension-producing effect of weak ipsilateral stimuli for the low spinal preparation—an effect which is not seen usually in the case of weak ipsilateral reflexes, but may be brought to light by the simultaneous combination with a contralateral extension-reflex. When the two antagonistic stimuli are of constant strength in a series of reactions, but when the contralateral extension-producing stimulus is applied at ever greater intervals of time after the commencement of the flexion-reflex, it is found that an optimum interval exists at which the extensor augmentation is greatest, and that thereafter and with greater intervals the augmentation is less. Very rarely a slight flexor augmentation may occur at the commencement of the period of double stimulation when a contralateral stimulus interrupts a weak flexion background.

The successive ("terminal") effects of double stimulation in recent spinal preparations may be summed up by saying that there appears to be an increase in the factors of extension activation immediately after the end of the period of double stimulation in compound reactions.

Where the two antagonistic stimuli are synchronously withdrawn this may appear as an "extensor rebound contraction." This may be evidenced in the compound reaction when present in neither "pure" reflex. Or, if present in either "pure" reflex, it may be found to be augmented in the compound reaction. It seems to increase in extent with increase in the strength of the contralateral extension-producing stimulus.

This extension successive effect is well seen against "backgrounds" of extension or of flexion. Such a "background" may be made by prolonging the contralateral or the ipsilateral stimulus unbroken after the period of double stimulation. When the ipsilateral flexion-reflex is so prolonged the successive extension effect following the double stimulation on withdrawal of the contralateral stimulus is seen in a failure of the flexor muscle to regain the level of contraction which would normally be conditioned by the "pure" ipsilateral stimulus. Quite often there is no flexor restitution at all. When it occurs it is usually of small extent, and is rarely complete. The extent of this flexor depression after double stimulation seems to be greater the relatively weaker the ipsilateral flexion-producing stimulus is, and greater also the later in the period of flexion stimulation the contralateral stimulus falls. Sometimes on withdrawal of the contralateral stimulus at the end of the period of double stimulation there is an additional relaxation of the flexor, and this perhaps corresponds to a "flexor terminal relaxation after inhibition" and is the reciprocal of an "extensor terminal (or "rebound") contraction after excitation."

When the "background" of extension is used this extension effect after double stimulation may be seen in an augmentation of extensor contraction. The cessation of the ipsilateral stimulus at the end of the period of double stimulation may be followed by a continued depression of the extensor contraction. This occurs when the period of double stimulation is a long one, or when the ipsilateral stimulus is relatively strong, or when it is applied some time after the commencement of the contralateral stimulus. In other cases there may be complete restitution of extensor contraction, while there may even be augmentation. This may occur when the period of double stimulation falls soon after the commencement of the contralateral stimulus, and the extensor augmentation may take the form of an extensor rebound contraction of transient form—although none is present after the simple flexion-reflex. Extensor augmentation after the end of the phase of double stimulation may appear even when the contralateral extension-producing stimulus is subliminal.

In de-afferented low spinal preparations general phenomena similar to those in the normal preparations have been noticed. In one case at the commencement of the period of double stimulation—a weak flexion-reflex then being in action—there appeared to be a slight augmentation of flexor contraction, then followed by a well-marked extensor contraction.

In the recent spinal preparation there sometimes occurs an abnormal crossed flexion-reflex, and the phenomena when this is compounded with the normal direct flexion-reflex are of interest. With weak stimuli, and when they are commenced together, there is sometimes an augmentation of the flexor contraction; but if the contralateral stimulus which gives the abnormal crossed flexion be applied during a normal ipsilateral flexion-reflex, there is often a depression of the flexor contraction during the period

of double stimulation. If a contralateral stimulus be first applied, a certain degree of flexor contraction is conditioned. When, during this stimulation, the ipsilateral stimulus is added, there may be an increase in the extent of flexor contraction—but not to the level which obtains in the "pure" ipsilateral reflex. If, then, the contralateral stimulus be withdrawn, there is a further increase in the flexor contraction—very nearly to the extent of the "pure" ipsilateral reflex. On the other hand, if the ipsilateral stimulus be first applied, there is a reduction of the flexor contraction during double stimulation, and on further withdrawal of the ipsilateral stimulus there is a still greater depression of flexor contraction; but the extent of flexor contraction which then obtains is greater than that in the "pure" contralateral reflex.

This result, which has been briefly mentioned in a previous paper (5), seems to be an evidence of the presence of two antagonistic factors (flexion activity and extension activity) which accompany the stimulation of a single afferent nerve of the hind limb—in this case the contralateral long saphenous nerve. When stimulated alone it produces a certain amount of flexor contraction which may be looked upon as conditioned by an overbalance of activation over inhibition in the flexor half-centre. But when placed against a background of greater flexion it may be that the inhibition factor is rendered more evident. A result certainly suggested by the relaxation of the flexor contraction of the "background" ipsilateral flexion-reflex when the contralateral stimulus is applied.

The general results of the compounding of reflexes as examined in this paper seem to indicate that, upon the whole, "algebraic summation" occurs when two antagonistic stimuli are compounded together, and that the value of the effects when two stimuli are compounded varies not only with their relative values but also (when their strengths are kept constant) with the time relations of the two stimuli when one is started before the other. In other words, the state of the centres may be altered by the previous application of one or other stimulus, and then the effects of double stimulation (the antagonistic stimulus simply being added to that first applied) vary with the length of time which the first stimulus has run alone and with the nature of that stimulus (ipsilateral or contralateral). This seems to shew that the state of the centres gradually changes during the application of a "pure" stimulus composed of a rapid series of faradic shocks of apparently constant strength.

But algebraic summation seems not always to be obtained. This has been seen on a few occasions in the case of the extensor muscle, which may shew greater contraction during double stimulation than in the "pure" extension-reflex. In these instances, perhaps, the factor of extension in the flexion-reflex and that of extension in the extension-reflex summate to give a greater extensor contraction than in either. If this is the case, it is significant that the effect is seen at its greatest when the extension-reflex is added to the flexion-reflex some time after the commencement of the

latter, as the factor of extension in the flexion-reflex of "decerebrate" type is seen usually late in the period of stimulation.

Of the successive effects of double stimulation in the spinal preparations, the most marked is an increase of extension activity after double stimulation, seen in either half-centre—in the flexor as flexor depression and in the extensor as extensor augmentation. This may perhaps be explained by saying that after double stimulation there is, against a background of flexion, an algebraic summation of that flexion and of the tendency to extensor after-discharge conditioned by the contralateral stimulus; and that against an extension background there is an algebraic summation of the continued extension and of an extensor rebound phenomenon conditioned by the cessation of the ipsilateral flexion-producing stimulus. Against a subliminal extension background this extensor augmentation has the appearance of the extensor rebound contraction of maintained type seen in decerebrate preparations, and this even when no such form is obtained on cessation of the "pure" flexion-reflex in the spinal preparation. Is it possible that the extension "background" to some extent reproduces the state of the centres in "decerebrate rigidity," and that the tendency to extensor rebound contraction after the flexion-reflex is masked in the low spinal preparation as a rule, but may then be evidenced against the subliminal extension background?

## XI. Summary.

1. In the present paper the immediate and successive effects of the compounding of stimuli have been examined in spinal preparations (low spinal and decapitate) as well in the de-afferented condition as in the normal.

2. During double stimulation (immediate effects) there is usually an algebraic summation of the "pure" reactions. This is such—as Sherrington has already pointed out—that the stronger the ipsilateral stimulus relatively is, the greater is the effect of extensor relaxation and flexor contraction during double stimulation; and the stronger the contralateral stimulus is, the greater is the effect of flexor relaxation and extensor contraction.

3. When the time relations of the antagonised stimuli are changed, it is found upon the whole that the extension effect during double stimulation is greater the later a contralateral stimulus falls in the period of ipsilateral stimulation; and that the greater is the flexion effect the later an ipsilateral stimulus falls in the period of contralateral stimulation. But often the flexion effect is much greater when the two stimuli are commenced synchronously than when the ipsilateral is commenced a short time after the contralateral.

4. Very rarely a slight augmentation of flexor contraction is seen at the commencement of the period of double stimulation when a contralateral stimulus is compounded against a background of weak flexion.

5. Less rarely an actual augmentation of extensor contraction occurs during double stimulation, so that this is greater than in the "pure" extension-reflex.

6. This effect is, within limits, proportional to the relative preponderance of the strength of the contralateral stimulus. But if this be changed by weakening the strength of the ipsilateral stimulus, it is found that there exists an optimum relation of the strengths of the two stimuli, and that a further decrease of the strength of the ipsilateral stimulus is accompanied by a reduction of the augmented extensor contraction.

7. It is also found that, within limits, this extensor augmentation of contraction during double stimulation is greater the later the contralateral stimulus falls in the period of the ipsilateral. But here too an optimum interval of time between the commencement of the ipsilateral stimulus and that of the interrupting contralateral exists. If the contralateral stimulus be applied at a greater interval of time, the extensor augmentation is decreased.

8. Even where the "pure" contralateral reaction evokes abnormal flexion there may be flexor depression during double stimulation. This is seen where the strength of the ipsilateral stimulus is comparatively great. Where the two antagonistic stimuli are small, or subliminal, there may be flexor augmentation of contraction.

9. The successive effects of the compounding of stimuli, as seen after withdrawal of one of the stimuli in the phase of double stimulation, seem chiefly to consist in flexion depression and extension augmentation.

10. This is seen in the tendency for only a partial restitution of flexor contraction to occur when the ipsilateral stimulus is prolonged after the period of double stimulation. Sometimes no restitution of flexor contraction may occur. When it does occur, it seems to be greater the relatively greater is the strength of the ipsilateral stimulus.

11. It is also seen in the tendency for extensor augmentation to occur when the contralateral stimulus is prolonged after the period of double stimulation. This is less the relatively stronger the ipsilateral stimulus is.

12. These points mentioned in this summary are some of the chief ones described in this paper, but it is impossible to summarise briefly all the various observations contained in it.

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STUDIES IN THE PHYSIOLOGY OF THE NERVOUS SYSTEM. XV.: IMMEDIATE REFLEX PHENOMENA RESULTANT UPON COMPOUND STIMULATION IN DECEREBRATE PREPARATIONS. By T. GRAHAM BROWN (Manchester). (With thirty figures in the text.)

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# STUDIES IN THE PHYSIOLOGY OF THE NERVOUS SYSTEM. XV.[1]: IMMEDIATE REFLEX PHENOMENA RESULTANT UPON COMPOUND STIMULATION IN DECEREBRATE PREPARATIONS.

By T. Graham Brown (Manchester).[2]

(With thirty figures in the text.)

(*Received for publication* 23*rd July* 1913.)

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## I. Introduction.

In the preceding paper of this series the immediate and successive phenomena in the compounding of two antagonistic reflexes were studied in the spinal preparations of the cat. Here only the immediate effects of

[1] The preceding papers have appeared in this Journal: vol. ii., No. 3, p. 243, 1909; vol. iii., No. 1, p. 21, 1910; vol. iii., No. 2, p. 139, 1910; vol. iii., No. 3, p. 271, 1910 (in collaboration with Miss Abel); vol. iii., No. 4, p. 319, 1910; vol. iv., No. 1, p. 19, 1911; vol. iv., No. 2, p. 151, 1911; vol. iv., No. 3, p. 273, 1911; vol. iv., No. 4, p. 331, 1911; vol. v., No. 3, p. 233, 1912; vol. v., No. 3, p. 237, 1912; vol. vi., No. 1, p. 25, 1913; vol. vi., No. 3, p. 209, 1913; vol. vii., No. 3, p. 197, 1913.

[2] The expenses of this research have been defrayed by a grant from the Carnegie Trust. The work was done in the Physiology Laboratory of the University of Liverpool during the tenure of a Carnegie Fellowship.

the compounding of the same two reflexes are dealt with, the condition in this case being the "decerebrate."

Sherrington has examined some of the immediate phenomena of simultaneous spinal induction in the decerebrate condition. He shewed, in the first place, that when the ipsilateral stimulus is pitted against the contralateral the contraction of the extensor is found to give place to inhibitory relaxation (1). The inhibiting ipsilateral stimulus may be applied either to a skin afferent or to a muscle afferent (hamstring nerve). Similarly, a contralateral stimulus may cause inhibitory relaxation of a reflex contraction of a flexor muscle.

He further shewed (2) that when the two stimuli are fairly strong the ipsilateral is prepotent. But if the ipsilateral stimulus is comparatively weak, the contralateral reaction (extensor contraction) may be exhibited. The extent of the resultant contraction of the extensor muscle during double stimulation, in fact, is dependent upon the relative values of the two antagonistic stimuli. It is further dependent upon their temporal arrangement; for the extent of contraction during the period of double stimulation may vary even when the stimuli are, in different reactions, of constant strength—this variation depending upon whichever of the two stimuli is first applied.

In a later paper Sherrington (3) again discusses the immediate phenomena in "double reciprocal innervation"—here in both spinal and decerebrate preparations. He there shews, for the decerebrate preparation, that this "algebraic summation" in the response to varied antagonistic stimuli may be demonstrated for the flexor as well as for the extensor of the knee. An interesting point in connexion with the experiments described in this paper is the presence of "tremor" during the period of double stimulation.

Still more recently, Sherrington and Sowton (4) have again examined the phenomena during double stimulation, as evidenced in the knee muscles. They confine themselves to the effect of interrupting a "background" of flexion with an intercurrent extension-producing stimulus. When that latter stimulus is weak, they find that it may produce an augmentation of flexor contraction, a phenomenon which has also been noticed by the author (6) in the case of antagonists at the ankle. Stronger contralateral stimulation (extension-producing) gives the more typical flexor relaxation, and this increases in value with increase in the strength of the interrupting stimulus. With constant contralateral stimuli increase of the strength of the "background" stimulus may give an augmentation of flexion during double stimulation, and decrease of it may give flexor relaxation. If the contralateral stimulus is repeated at intervals, they find that the inhibitory effect is greater later in the period of the flexion stimulus, and lesser earlier in that period.

## II. Methods Employed.

The methods employed in these experiments have been similar to those described in previous papers of the series. The cats used have been rendered unconscious before the commencement of the experiment, and have been kept completely unconscious until destroyed at the end of it.

In stimulating the afferent cutaneous nerves used throughout (long saphenous nerves), I have used electrodes which have two large platinum poles set comparatively far apart, but lately a new pair of electrodes has given excellent results.

These are a modification of the ordinary tripolar electrodes. A large platinum plate has placed upon it an oval disc of vulcanite, and the edges of the plate are turned up all round over the edge of the vulcanite disc for a distance of about 2 mm. In the long direction of the disc there is a shallow groove, and at the ends of this groove the platinum plate (which there is somewhat elongated) is turned up for a distance of about 4 mm. into the groove at each end. To the plate is welded a guarded wire. In the centre of the groove there is an isolated plate of platinum about 8 mm. long, and to the side of this is welded a second guarded wire. The two wires are connected in the ordinary manner to the poles of the inductorium.

Before this electrode is used the nerve is first laid free for a sufficient distance, and then the electrode is slipped between it and the underlying muscles. The nerve lies in the groove. Thus the nerve is in contact with three poles, and of these the peripheral and spinal are also in contact—by means of the platinum plate on the under-surface of the electrode—with the neighbouring tissues. As regards the body of the animal, this plate forms an "indifferent" electrode such as is used in "unipolar" stimulation; but the nerve itself lies between three ordinary tripolar electrodes. The middle electrode is isolated by the vulcanite from the tissues of the animal, and its wire is not allowed to come into any contact with the animal. Hence when the surface of the vulcanite is wet, any spread of current from the central electrode first arrives at the peripheral rim of platinum—that is to say, that it passes straight to the other electrode without passing across any part of the surrounding tissues.

These electrodes are extremely satisfactory in preventing "spread" when strong currents are used. With the strongest currents which the coils give there is no trace of "spread." With ordinary guarded bipolar electrodes a certain proportion of the stimulating current passes up the nerve from one pole, passes through the tissues behind the electrode, and then passes up the nerve from below to the other pole. Again, "spread" may occur across the wet surface of the vulcanite. With strong currents this may cause the underlying muscles to contract, and sometimes currents strong enough to give this contraction have to be used. With tripolar electrodes "spread" may occur over the surface of the vulcanite if it is wet —as it almost always has to be. But even in these circumstances no

"spread" should occur with the electrodes here described. However, when they are in use the nerve is usually covered with a piece of damp cotton wool, and it is possible that—if this overlaps the electrode—"spread" may occur through the saline solution with which the wool is damped. But if this method is used and the "spread" does occur, the large size of the "indifferent" electrode (that is, the platinum plate) prevents concentration of the current in a small piece of tissue, and the stimulating effects of the "spread" are not seen.

## III. Stimuli of Synchronous Commencement.

In these experiments the two compounded stimuli have with comparative rarity been applied at the same time and terminated also synchronously. If, however, antagonistic stimuli one of which gives ipsilateral flexion and the other contralateral extension be compounded in this manner, upon the whole the resultant reaction demonstrates algebraic summation between the two "pure" reflexes.

Thus the ipsilateral stimulus when applied alone may evoke a reaction of ipsilateral flexion characterised by flexor contraction of "spinal" form and by extensor relaxation; and the contralateral stimulus may evoke a reaction in which the extensor shews contraction of "spinal" form accompanied by a very slight flexor relaxation. But when both the stimuli are applied synchronously, the flexor contraction may become smaller than before, and during the application of the double stimulation the extensor also may shew contraction. This contraction commences later than the extensor contraction in the "pure" extension-reflex. It rises more slowly, and often the curve is of irregular outline.

A typical form of the extensor contraction during double stimulation is one in which the movement commences gradually, and slowly increases in extent as the period of double stimulation is prolonged (fig. 1). In such instances the flexor shews a reciprocal diminution of the extent of its contraction as the period of double stimulation is prolonged.

Interesting variations of this course of events may occur. For instance, in one case the "pure" contralateral reaction was one of extension of "spinal" type. When both stimuli were applied synchronously the initial flexor contraction was of greater extent than in the "pure" flexion-reflex. There was a synchronous sharp relaxation of the extensor which was not present in the "pure" flexion-reflex. This lasted for about 0·5 second, and thereafter the extensor rose in contraction at first rapidly and then more slowly. At the same time the flexor relaxed—at first rapidly and then more slowly (fig. 2). In this reaction the form of the extensor contraction resembled the "decerebrate" type, in which a brief relaxation precedes extensor contraction—although the "pure" extension-reflex was of "spinal" type. Later in this same experiment the "pure" flexion-reflex was of a type in which there was an increase in the extent of flexor contraction late

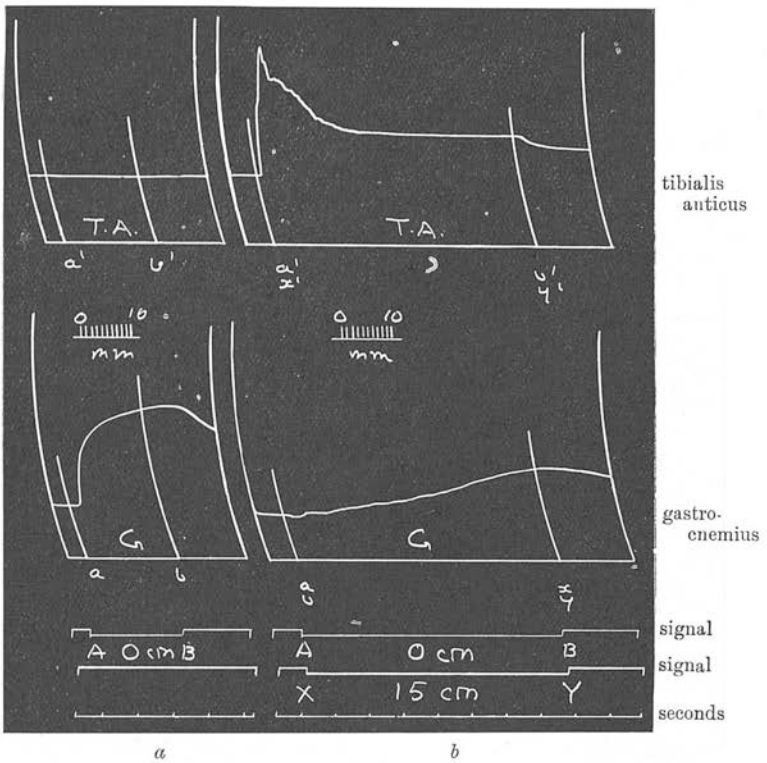


FIG. 1.—Experiment C, cxl., record 258, 6032; 26/11/12.—Decerebrate cat, reactions obtained 1 hour and 46 minutes after decerebration—an interval of 1 minute between *a* and *b*.

Reaction *a* is a "pure" crossed extension-reflex. In reaction *b* ipsilateral and contralateral stimuli (long saphenous nerves) are synchronously compounded. The compound reaction exhibits a typical slow rise of the curve of contraction of the extensor. A reciprocal fall in the flexor curve takes place. The curve of flexor contraction in a "pure" ipsilateral flexion-reflex was well sustained.

In this, and in all succeeding figures, the fall of a curve denotes relaxation, and the rise contraction of the registered muscle. The upper tracing is obtained from the flexor (tibialis anticus), and the lower from the extensor (gastrocnemius). Below these two tracings are the signal lines. The beginning of stimulation and the end are there marked by capital letters (X–Y for ipsilateral stimulation [lower signal] and A–B for contralateral stimulation [upper signal]); and ordinates ($x$, $x'$; $y$, $y'$: $a$, $a'$; $b$, $b'$), which correspond in time with these points, have been drawn upon the two muscle tracings. Other ordinates (marked with figures) have in some cases also been drawn in order to demonstrate other time relations. On the curves, millimetre scales have been drawn before varnishing; these are therefore reduced in proportion with the tracings. Time is marked in seconds upon the lowest line. [It must clearly be noted that the ordinates thus drawn upon the tracings are only approximately correct, as they have to be added when the paper is sent round the kymograph a second time, and as it then sometimes falls or rises when not accurately cut. This has been compensated—as far as is possible without undue waste of time in an experiment—by raising or lowering the recording levers at the time of making these ordinates. If the necessity for exact time relations should ever arise, these may be obtained from the pair of ordinates at the beginning or at the end of a record. These are made on the stationary drum immediately before and immediately after each record. At the same time the signal levers are also made to record. All other ordinates save these should be regarded as drawn for convenience of demonstration only, unless checked against the initial or terminal ordinates of a reaction.]

in the period of stimulation, and this was accompanied by an extensor contraction—so that, as happens rarely, the two antagonists simultaneously exhibited a state of increasing shortening. When the two antagonistic stimuli were then synchronously applied the late flexor augmentation was diminished in extent while the late extensor contraction was increased (fig. 3).

But algebraic summation does not always hold good for this form of

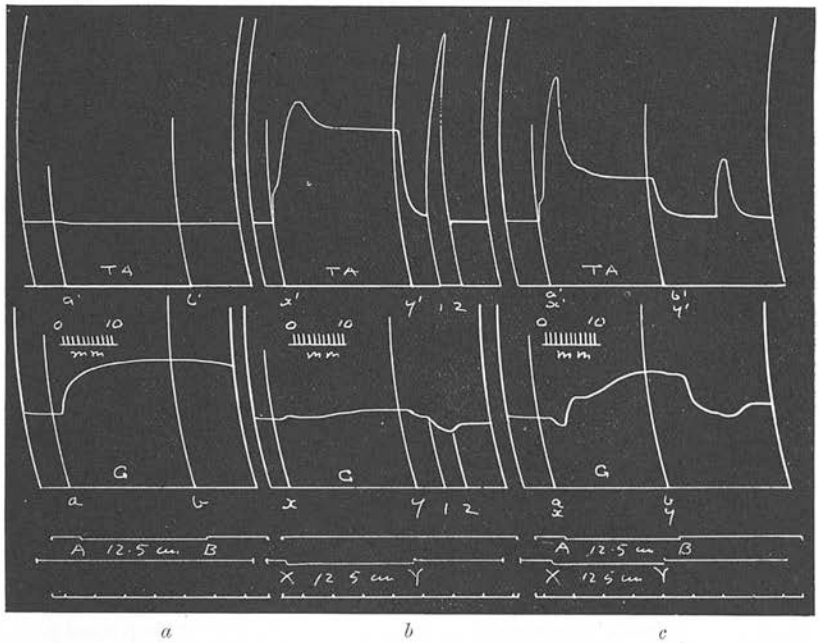


FIG. 2.—Experiment C, xxxiii., record 58, 1560; 10/4/11.—Decerebrate cat. Three reactions obtained 3 hours and 20 minutes after decerebration; 1 minute intervals between *a*, *b* and *b*, *c*.

Reaction *a* is a "pure" contralateral extension-reflex of "spinal" type. Reaction *b* is a "pure" ipsilateral flexion-reflex of somewhat "decerebrate" type—note the flexor rebound contraction after excitation. Reaction *c* is compounded of the two. Here the flexor contraction is at first greater than in the "pure" flexion-reflex, but more rapidly falls—the flexor rebound contraction occurs later and is reduced in extent. In the extensor tracing there is at first a marked preliminary relaxation. This then gives place to contraction which is, however, not so great as in the "pure" extension-reflex. This tracing resembles that of an extension-reflex of "decerebrate" type.

compounded reaction. Even where there is a marked extensor contraction in the "pure" extension-reflex, when the same stimulus is applied synchronously with an antagonistic ipsilateral one, the extensor contraction may be entirely suppressed [see xvi., fig. 1, reaction *b*].[1] This has been observed to occur when the reactions were of "spinal" form, and even when the extension-reflex was well marked at the strength of contralateral stimula-

[1] In this and the following papers references are made to figures in the others. For convenience the number of the paper in the series only is given (Roman numerals). Thus figure 3 in this paper is referred to as "xv., fig. 3." The above reference therefore means —"see fig. 1, reaction *b*, in the sixteenth paper of this series; that is, the paper which immediately follows the present one."

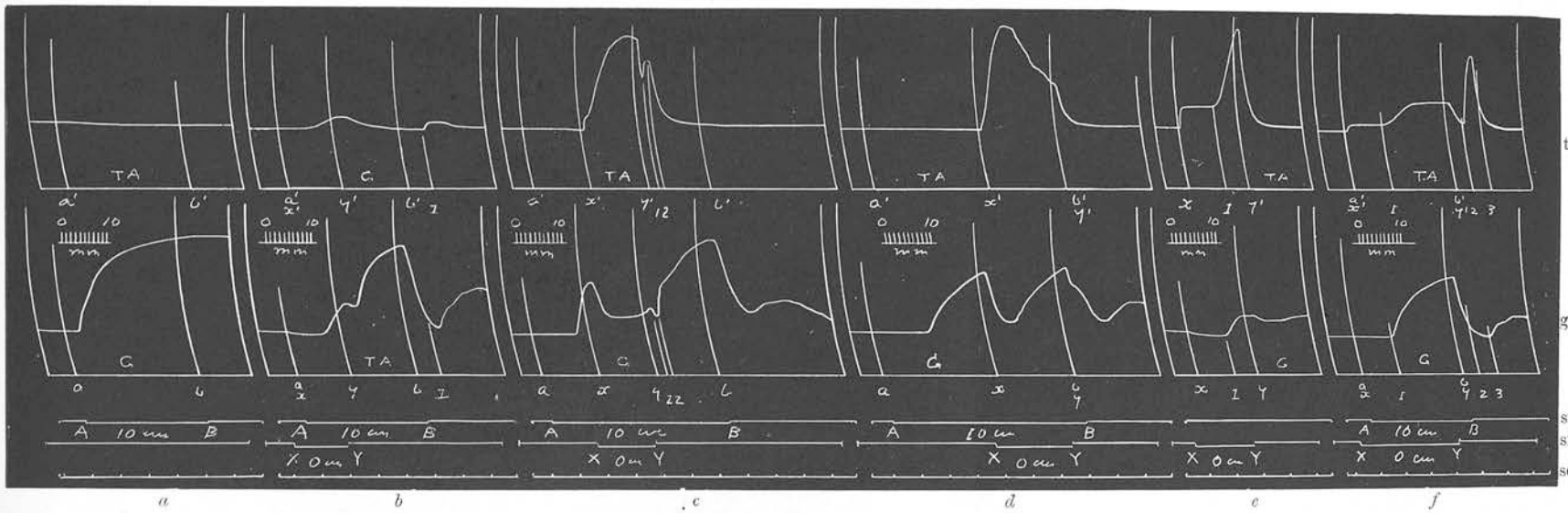


FIG. 3.—Experiment C, xxxiii., record 58, 1581 : 10/4/11.—Decerebrate cat, six reactions obtained 3 hours and 59 minutes after decerebration—an interval of 1 minute between them ; except between *b* and *c*, where the interval is one of 2 minutes. The same strengths of stimuli used throughout.

Reaction *a* is a "pure" contralateral extension-reflex—note the "tonic" extensor after-discharge.

Reaction *b* is compound ; extension "background," stimuli commenced synchronously but ipsilateral first withdrawn. Note slight flexor contraction and complete suppression of extensor contraction during first part of double stimulation, then commencing extensor contraction ; after end of double stimulation, slight extensor relaxation and then recovery of it ; after withdrawal of "background" stimulus, extensor relaxation accompanied somewhat later by flexor rebound contraction (not present in "pure" ipsilateral reflex—*e*)—then late partial reconstitution of the tonic extensor after-discharge.

Reaction *c* is similar to *b*, but double stimulation falls later in the period of the "background" stimulus. Note during double stimulation less complete extensor relaxation than in *b*, but much greater flexor contraction (greater than in "pure" flexion reflex). Compare the features in third phase (ordinates *y*, *y'* ; *b*, *b'*) with those in *b*, and note flexor rebound (at ordinates 1, 2). Note extensor relaxation on withdrawal of contralateral stimulus, and less marked reconstitution of extensor tonic after-discharge than in *b*.

In reaction *d* the double stimulation falls later, and the stimuli are terminated synchronously. Note the smaller value of extensor relaxation during double stimulation than in *b* or *c*. Note also the greater extent of extensor contraction in the latter part of the period ; and note the comparatively sharp fall of extension on withdrawal of the two stimuli.

Reaction *e* is a pure flexion-reflex in which there is irreciprocal contraction of flexor and extensor towards the end of the period of stimulation. (Earlier in this experiment flexor rebound was present on cessation of the ipsilateral stimulus.) Reaction *f* is compound, and it will be observed that the same phenomenon of irreciprocal contraction occurs, but that the flexor component is reduced and the extensor increased. There is here a flexor rebound contraction not present (at this period of the experiment) in the "pure" flexion-reflex.

This figure demonstrates, amongst other things, an instance in which against an extension "background" the extensor relaxation during double stimulation is less the later that period falls in the course of the extension-reflex. It also demonstrates some phenomena of the third phase—including the appearance of flexor rebound ; and, in the fourth phase, extensor relaxation, although that is seen neither in the "pure" flexion-reflex nor in the "pure" extension-reflex.

tion used. There was no contraction of the extensor during the period of double stimulation, but the flexor contraction was smaller than in the "pure" flexion-reflex.

### IV. Stimuli of Asynchronous Commencement—Contralateral Extension - Reflex ("Background") preceding Ipsilateral Flexion-Reflex ("Interruptor").

The effects of the compounding of stimuli are best studied when one stimulus is first applied, and then (during the continued application of the first) a second stimulus of antagonistic effect is added. In such records the state of the "pure" reaction immediately changes over into the state of the compounded reaction. But it must be noted that the effects of compounding two stimuli of unchanged value may not be the same when they are both started together and when the one is started one or two seconds after the commencement of the other—for the state of the centre first activated may change during the application of the first stimulus applied, so that the second stimulus is applied in different phases of activity of the two linked "half-centres." In these experiments the second stimulus has generally been commenced two seconds after the commencement of the first; but the temporal relationships of two constant antagonistic stimuli have sometimes been changed in series of reactions. In other series the temporal relationships have been kept constant, and the value of one of the antagonistic stimuli compounded has been progressively altered.

In general, when a contralateral extension-producing stimulus is first applied, relaxation of the extensor contraction thus conditioned is the resultant of the subsequent application of an ipsilateral flexion-producing stimulus during application of the first. At the same time a flexor contraction is conditioned by the second stimulus. But the extensor relaxation is not complete, and the flexor contraction is not so great as in the "pure" ipsilateral flexion-reflex evoked with the same strength of ipsilateral stimulation. There is thus in such cases algebraic summation of the two effects (see fig. 14; also xvi, fig. 1).

But it occasionally happens that the ipsilateral stimulus when applied during the application of the contralateral gives a complete relaxation of the extensor contraction, and this relaxation may even be down to a level below the level of "rest" of the muscle (see fig. 9). Such cases occur when the strength of contralateral stimulation is comparatively weak, and that of ipsilateral stimulation comparatively strong.

It also may happen that, although the ipsilateral stimulus gives a flexion contraction when applied "pure," yet when given during the application of a contralateral stimulus there is no evident flexor contraction although there is a partial relaxation of the extensor contraction. This has been observed when the ipsilateral stimulus is comparatively

weak. In one instance it was observed to occur during a period in which the decerebrate preparation was in process of micturition and defecation. During this the contralateral extension-reflex seemed not to be impaired, but there was a reduction of the extent of the ipsilateral flexion-reflex. When the ipsilateral stimulus was applied "pure" there was still a flexor contraction. If, however, the ipsilateral stimulus was commenced two seconds after the commencement of the contralateral, the extensor contraction was somewhat reduced in extent but there was no corresponding flexor contraction.

Variations of the general rule may occur. Thus it occasionally happens that there may actually be an augmentation of the flexor contraction when the ipsilateral stimulus is commenced after the commencement of the contralateral (see fig. 3). In the instances in which this phenomenon has been observed the "pure" ipsilateral flexion-reflex has been of "decerebrate" type—during the period of stimulation there has been a slow and gradually increasing extensor contraction, and a reciprocal flexor relaxation. The contralateral extension-reflex was generally of "spinal" type, and the phenomenon usually occurred when the contralateral stimulus was of comparatively weak strength—although this was not always the case. When the ipsilateral stimulus was applied during the application of the contralateral the first effect was a rapid flexor contraction accompanied by a marked extensor relaxation. In some cases this relaxation was complete. [In neither the "pure" ipsilateral flexion nor in the "pure" contralateral extension was there a preliminary relaxation of the extensor.] Thereafter the flexor contraction diminished in extent and the extensor contraction gradually rose, but usually did not reach in extent to that of the "pure" extension-reflex. In some cases, however, the extent of extensor contraction during double stimulation was augmented, so that it was greater than in the "pure" extension-reflex. The extension "background" was weak, but the "pure" ipsilateral stimulus gave a marked flexion-reflex.

In series of successive reactions in which the time relations of the two stimuli are kept constant, but in which the value of one of the two compounded antagonistic stimuli is progressively altered, there may be a corresponding alteration in the phenomena which occur during the period of double stimulation.

Thus the interrupting ipsilateral stimulus may be of constant strength in such a series and the "background" contralateral stimulus may be increased in value in successive reactions. It then occurs that the extent of flexor contraction during the period of double stimulation is decreased, and at the same time the amount of extensor relaxation during double stimulation is also decreased. Again, the contralateral stimulus may be kept of constant value, but the ipsilateral stimulus may be increased in successive reactions. In such a case the flexor contraction and the extensor relaxation both increase in extent with comparative increase of strength of the ipsilateral stimulus (figs. 4, 5, 6, 21, 22) [see also xvi., fig. 9].

In series of reactions the strengths of the exciting stimuli may be kept constant, but their time relations may be changed. In such series the ipsilateral stimulus may be at first commenced in time with the commence-

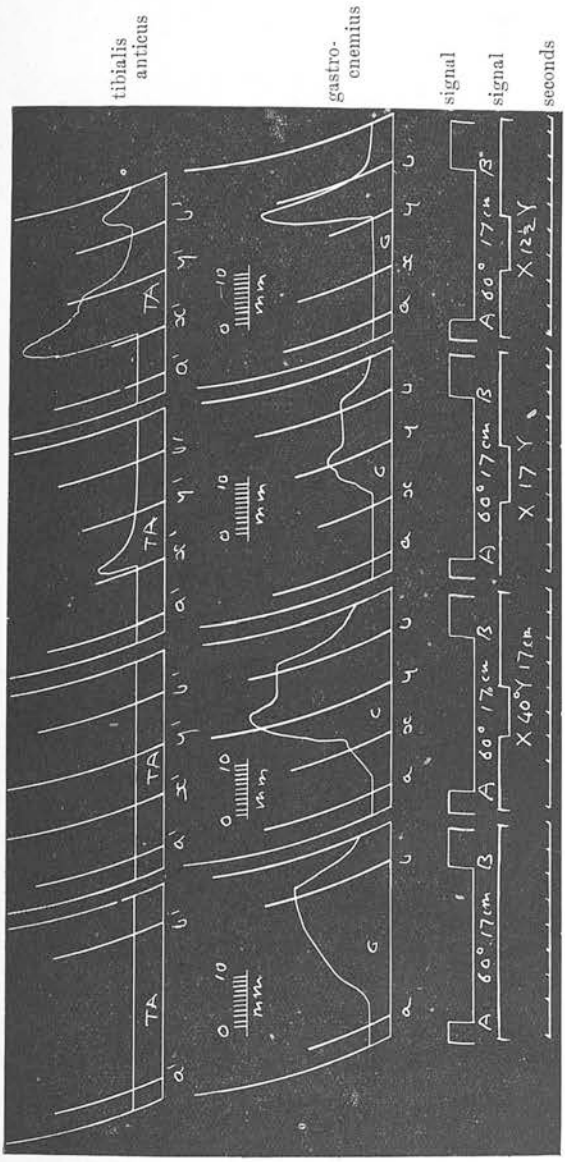


FIG. 4.—Experiment C, clxix., record 301, 7811 ; 28/2/13.—This and the two following figures are from the same experiment, and the reactions are directly successive in time. Decerebrate cat, a series of reactions obtained 4 hours and 28 minutes after decerebration ; minute intervals between successive reactions, and between the last reaction in one figure and the first in the following figure.

Reaction *a* is a "pure" contralateral extension-reflex taken at a strength of stimulation which is comparatively weak, and is the same as that used as a "background" in the three succeeding compound reactions. In these reactions—*b*, *c*, *d*—three different strengths of interrupting ipsilateral (flexion-producing) stimulation are used. It will be observed that a certain amount of "fatigue" of the extension background occurs—this is seen by the decreasing extent of extensor contraction in the first part of each compound reaction.

In reaction *b* extensor augmentation occurs during double stimulation. This is to a greater extent than in *a*. The "pure" ipsilateral reaction at this strength gave a flexion-reflex of "decerebrate" type—extensor contraction occurring during the latter part of the period of stimulation. In *c* fatigue of the extension-reflex has occurred. The period of double stimulation is characterised by a slight flexor, and a later extensor contraction. This is not so great as in *b*—it is nearly of the same extent and form as in the "pure" flexion-reflex evoked with the strength of ipsilateral stimulation used in *b*. In *d* a stronger ipsilateral stimulus gives a greater flexion which is unaccompanied by extensor contraction—note an extensor augmentation on withdrawal of the ipsilateral stimulus. This is to an extent of contraction greater than in the "pure" extension-reflex. Note also a flexor rebound contraction on withdrawal of the contralateral "background" stimulus.

ment of the contralateral, and then in successive reactions it may be applied at ever longer intervals of time after the commencement of the contralateral stimulus (figs. 3, 7).

When the two stimuli are at first applied simultaneously the resultant

flexor contraction is usually greater than when the ipsilateral stimulus is first applied in time soon after the commencement of the contralateral extension-reflex. At the same time, the amount of extensor relaxation is

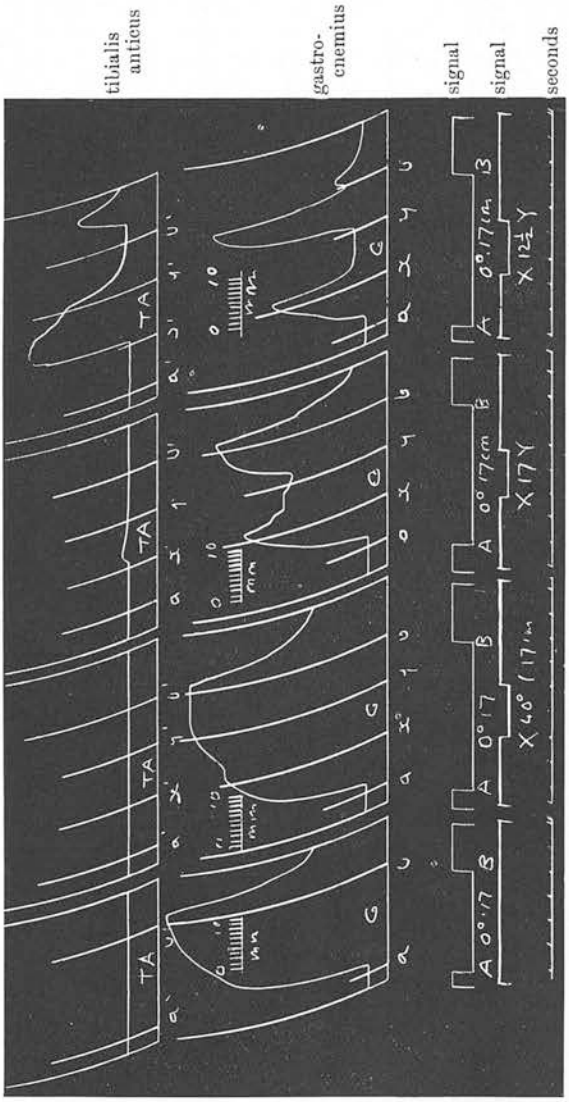


FIG. 5.—See fig. 4, a similar series from the same experiment but with a stronger "background" stimulus.

Reaction *e* gives this as a "pure" reflex. In reaction *f*—same ipsilateral stimulus as *b*—there is a slight depression of extension during double stimulation. In reaction *g*—same ipsilateral stimulation as *c*—there is a greater depression of extension. The level of extensor contraction during double stimulation is, however, higher than in *c*, and the flexor contraction is less. In reaction *h*—same ipsilateral stimulus as *d*—the extensor depression during double stimulation is again greater than in *g*. But it is slightly less than in *d*, and the flexor contraction is also less. Note that in *g* and *h* the extensor augmentation which occurs on withdrawal of the ipsilateral interrupting stimulus is greater than in *c* and *d*; also note that the flexor rebound on withdrawal of the contralateral stimulus (not present in *e*) is greater in *h* than in *d*.

also greater. If the ipsilateral stimulus be first commenced shortly after the commencement of the contralateral (say one second), the resultant flexor contraction is less than in the former case and the extensor relaxation is also less. As the interval between the two stimuli is then increased, the flexor contraction again becomes greater, and so also does the extent of extensor relaxation, the relationships of the variations of flexor

contraction and extensor relaxation therefore being reciprocal. It occasionally happens, however, that if the "pure" flexion-reflex shews

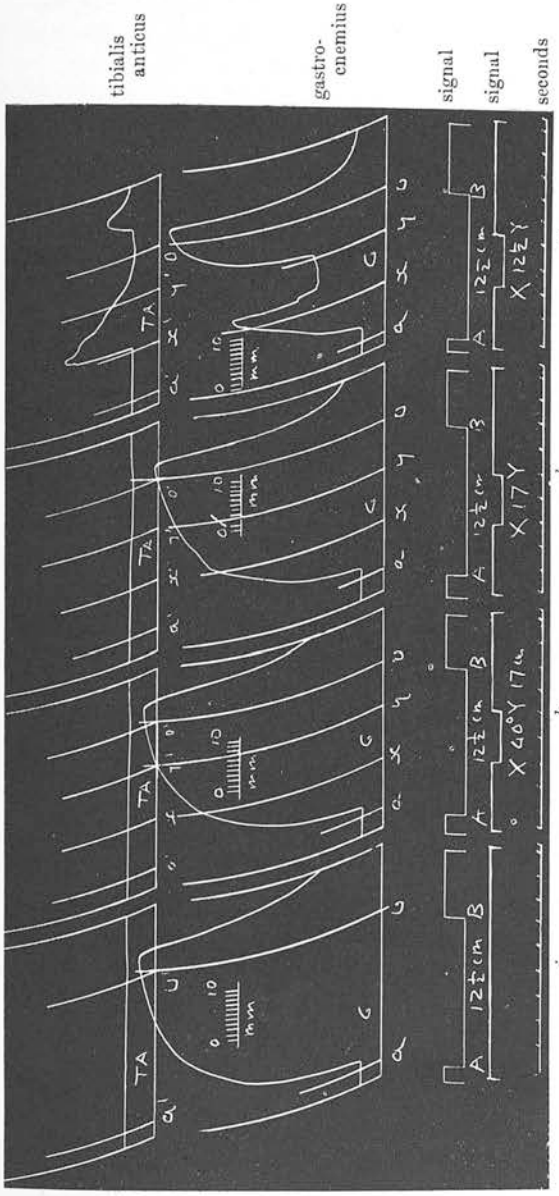


FIG. 6.—See figs 4, 5, a similar series, but with a still stronger "background" of extension.

Reaction *i* gives this as a "pure" extension-reflex. Reaction *k*—same strength of ipsilateral stimulus as *b* and *f*—shews no change during double stimulation. Reaction *l*—same ipsilateral stimulus as *e* and *g*—shews but a slight extensor depression, and this is unaccompanied by flexor contraction. Reaction *m*—same ipsilateral stimulus as *d* and *h*—shews a marked extensor relaxation during double stimulation. This is, however, less than in *d* and *h*. The reciprocal flexor contraction is also less. Note that the extensor restitution after double stimulation is greater than in *d* and *h*; and that the flexor rebound is about the same as in *d*. In a "pure" ipsilateral flexion-reflex taken with the same strength of stimulus as *d*, *h*, and *m* there was an extensor rebound contraction and no flexor rebound contraction

In each of these three figures there is demonstrated the effect of increasing the strength of the interrupting ipsilateral stimulus against a constant extension "background." The effect upon a constant interrupting stimulus of changing extension "backgrounds" is also demonstrated if the reactions *b*, *f*, *k*; *e*, *g*, *l*; and *d*, *h*, *m* be compared—for in each of these three sets the ipsilateral stimulus is of constant strength and the contralateral "background" is varied. The three figures together demonstrate an algebraic summation of flexion and extension ranging from *d*, where flexion is relatively strongest, to *k*, where it is relatively weakest. But in *b* algebraic summation is not shewn—there extensor contraction during double stimulation is greater than the sum of the extensor contractions in the "pure" ipsilateral flexion-reflex and contralateral extension-reflex.

a very slow flexor contraction, then the extent of flexor contraction in the compounded reaction is at its least when the two stimuli are commenced synchronously, and with increasing intervals of time between the commencements of the two stimuli then progressively increases. Yet it is remarkable

that at the same time the extent of extensor relaxation during double stimulation may decrease (fig. 3).

But, although the extent of extensor relaxation during double stimulation in some cases is greater the later the interrupting ipsilateral stimulus is applied in the course of the "background" stimulus, this is not so common an occurrence as its opposite. It seems to be the more general rule that the extensor relaxation is less the later the interrupting stimulus falls (figs. 3, 7) [see also xvi., figs. 8, 10, 21].

It is a curious point that, although the flexor contraction element during double stimulation when the ipsilateral stimulus is made to fall late in the period of the "background" contralateral stimulus may be as great as, or greater than, that element when both stimuli are commenced together, yet in the former case a marked element of extensor contraction may be present, whereas in the latter case it may be absent when stimuli of the same strength are used [see xvi., fig. 8]. In one case—where a liminal contralateral stimulus was used—the flexor contraction of double stimulation was greater the later the interrupting ipsilateral stimulus fell in the period of the contralateral. At the same time, an extensor contraction actually appeared during double stimulation. The temporal relations of the stimuli were changed in both directions—giving the same results [see xvi., fig. 20].

## V. Stimuli of Asynchronous Commencement—Ipsilateral Flexion-Reflex ("Background") preceding Contralateral Extension-Reflex ("Interruptor").

When the flexion-producing stimulus is first applied and the contralateral extension-producing stimulus is then commenced during its application, the general effect may be said to be a relaxation of the flexor contraction and either accompanied or not accompanied by an appearance of extensor contraction. The resultant flexor contraction of the compounded reaction is not so great as in the "pure" flexion-reflex, and the resultant extensor contraction is not so great as in the "pure" extension-reflex. There is, in fact, an algebraic summation of the two antagonistic effects.

Sometimes, however, the application of the contralateral extension-producing stimulus is accompanied by a complete relaxation of the flexor contraction and by an extensor contraction of nearly "pure" extent [see xvii., fig. 2]. In other cases, although relaxation of the flexor contraction may occur, there may be no evident contraction of the extensor, even when there is a fairly marked "pure" extension-reflex at the strength of contralateral stimulation used. In yet other cases, where the extension-reflex is slight at the strength of stimulus used, there may be little evident relaxation of the flexor and no evident extensor contraction when the two antagonistic stimuli are compounded. These several variations seem to depend upon the relative strengths of the two antagonistic stimuli.

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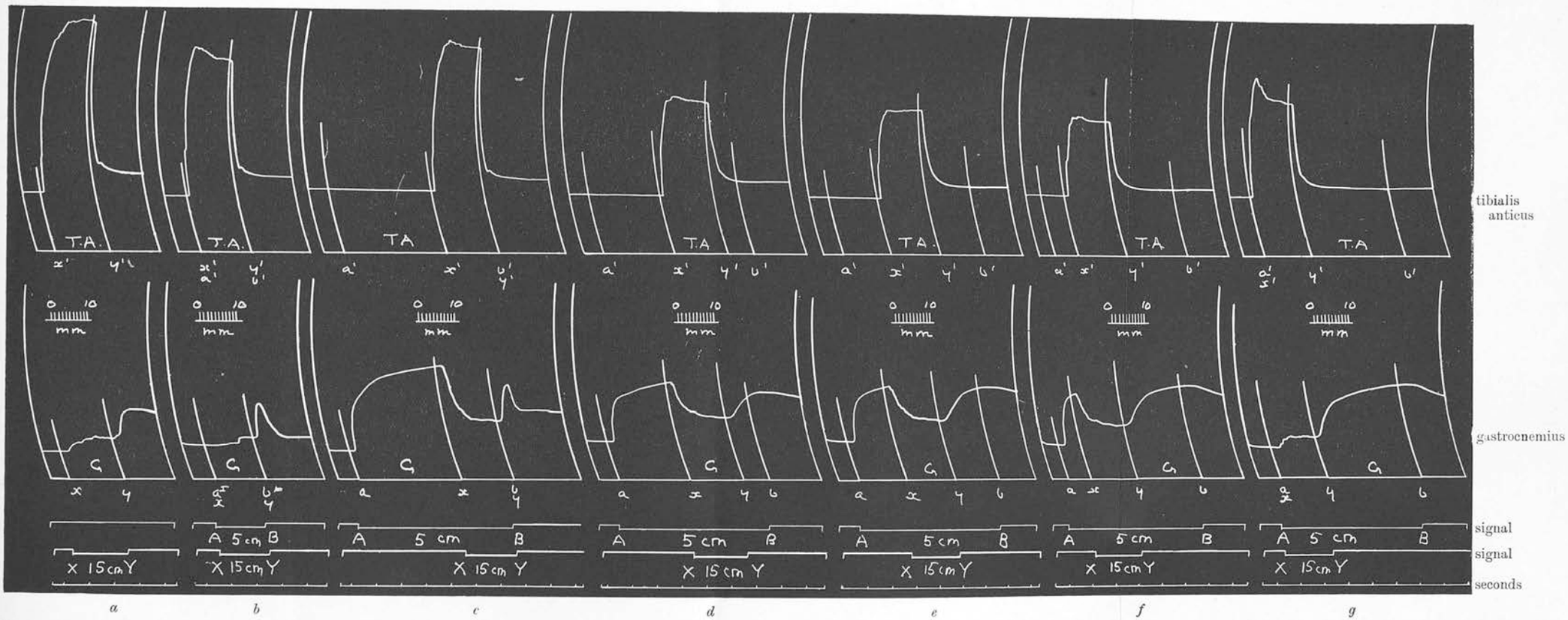


FIG. 7.—Experiment C, cxl., record 258, 6011 ; 26/11/12.—Decerebrate cat. A series of reactions obtained 1 hour and 24 minutes after decerebration, and taken at minute intervals.

Reaction *a* is a "pure" flexion-reflex. In *b* the compounding of the two stimuli is one of synchronous commencement and termination. In reaction *c* the ipsilateral stimulus is applied about 4 seconds after the commencement of the contralateral, while in *d*, *e*, and *f* the intervals are 3, 2, and 1 second respectively. In *g* the stimuli are again commenced synchronously. Note that the flexion effect is greatest when the stimuli commence synchronously and also when the interval between their commencements is great—whereas it is less when the intervals are short, being least when the interval between the commencement of the contralateral and ipsilateral stimuli is 1 second. Note, however, that it is again greater when the interval between stimuli is reduced to zero (synchronous commencement). It should be observed that a progressive "fatigue" seems to be present in this series.

About this time in the experiment the "pure" extension-reflex persisted as a tonic extension after-discharge on cessation of stimulation. In reaction *a* it is seen that the ipsilateral stimulus was followed by an extension rebound which also was tonically maintained. But note that when both stimuli are terminated together there is an extensor rebound contraction which gives place to relaxation and is not carried on at its greatest height as a maintained contraction.

A notable variation of the usual effects of compounding antagonistic ipsilateral and contralateral stimuli is that in which the application of a contralateral extension-producing stimulus during the application of an ipsilateral flexion-producing stimulus gives not flexor relaxation but actually flexor augmentation. An instance in which this occurred has already been published (6), and the phenomenon is not a very rare one.

Augmentation of the flexor contraction may occur when there is an element of flexor contraction in the contralateral extension-reflex, but it may also appear when the contralateral reaction is one of uncomplicated

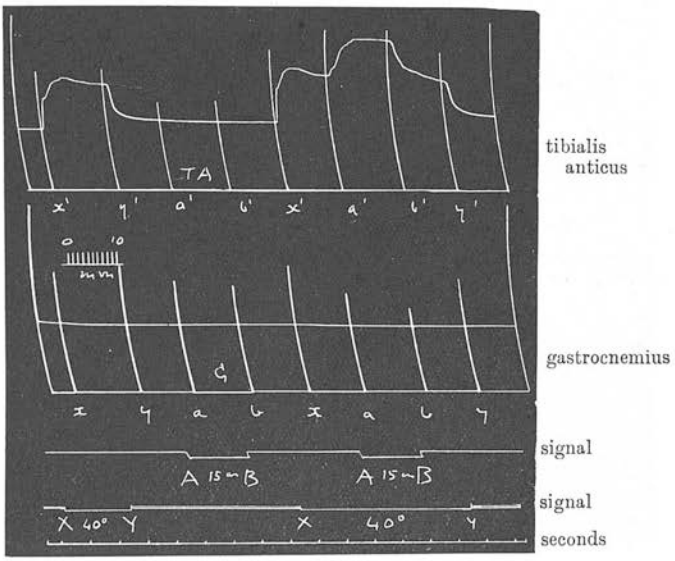


FIG. 8.--Experiment C, xxii., record 48, 1160; 16/3/11.—Decerebrate cat. A record obtained 3 hours and 27 minutes after decerebration.

A minimal ipsilateral stimulus is first applied and evokes a weak flexion-reflex. A sub-minimal contralateral stimulus then applied evokes no reaction. [This is not due to depression of extension following upon the ipsilateral stimulus, because this contralateral stimulus also failed to give any reaction when applied without preceding ipsilateral stimulation.] Thirdly, the ipsilateral stimulus is applied again and the contralateral is then compounded with it. Here there is a marked augmentation of flexion during double stimulation.

extensor contraction ("spinal" type). It is also sometimes seen when the contralateral stimulus, at the strength used, evokes no reaction. In an instance of this nature there was immediate flexor augmentation on commencement of the contralateral stimulus, and this augmentation lasted throughout the period of application of the two antagonistic stimuli; the ipsilateral stimulus was also a weak one (fig. 8).

Where the "pure" contralateral extension-reflex consists solely of extensor contraction uncomplicated by flexor contraction, the compounded reaction, in the phase of double stimulation, may be composed of an element of flexor augmentation with or without an element of extensor contraction. An instance of the latter type occurred in an experiment

in which, when the contralateral stimulus was first applied and the ipsilateral then given, there was a greater flexor contraction than in the "pure" flexion-reflex evoked at the same strength of ipsilateral stimulation; at the same time there was conditioned a reciprocal complete relaxation

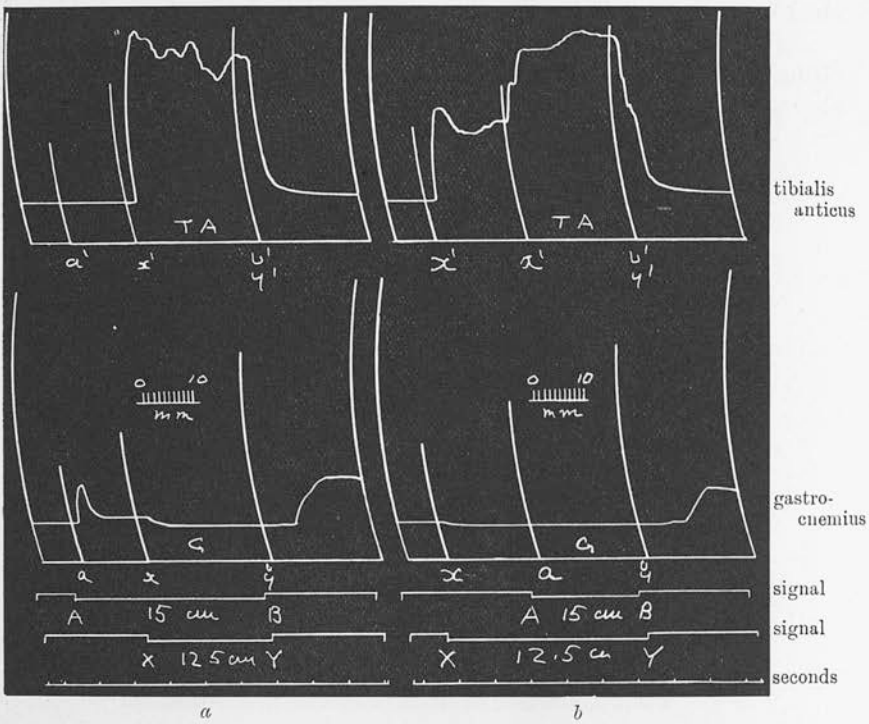


FIG. 9.—Experiment C, cxxvii., record 245, 5705; 7/11/12.—Decrebrate cat. Two reactions obtained 3 hours and 1 minute after decerebration, an interval of 1 minute between them.

In reaction *a* the contralateral stimulus is first applied, and during its application an ipsilateral stimulus is compounded with it. There is a relaxation of the extensor to a level below that of "rest." The flexor contracts to a level greater than that in the "pure" flexion reflex (as shewn by comparison with the first part of reaction *b*). In reaction *b* the ipsilateral stimulus is first applied. When the contralateral is compounded with it there is an augmentation of flexor contraction and no change in the extensor curve. In these two reactions, the first part of *a* gives a "pure" extension-reflex, and the first part of *b* gives a "pure" flexion-reflex. Note the extensor rebound on cessation of stimulation. This was not present in the "pure" flexion-reflex, but in the "pure" extension-reflex there was an extensor after-discharge of considerably smaller extent and less good maintenance than this rebound contraction.

of the extensor contraction which was evoked in response to the contralateral stimulus (fig. 9). When the ipsilateral stimulus was first applied it then evoked a flexor contraction accompanied by a slight extensor relaxation. During its application a contralateral stimulus was then compounded with it. There was an immediate flexor augmentation accompanied by a slight additional extensor relaxation. The augmentation of flexor contraction persisted throughout the period of double stimulation,

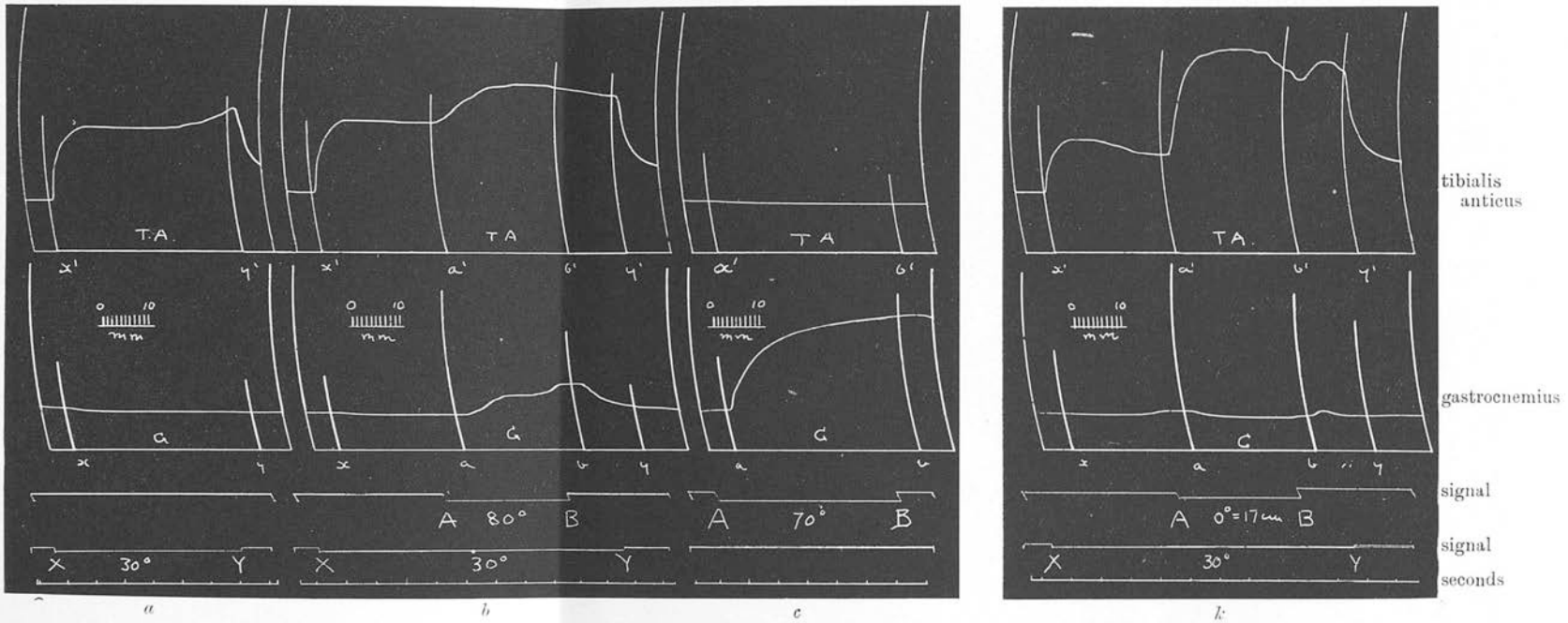


FIG. 10.—Experiment C, XXV., record 46, 1111 ; 15/3/11.—Decerebrate cat. A series of reactions obtained 6 hours and 15 minutes after decerebration. An interval of 1 minute between *a* and *b*, of 4 minutes between *b* and *c*, and of 7 minutes between *c* and *k*

Reaction *a* is a "pure" ipsilateral flexion-reflex taken at the strength of ipsilateral stimulation used in the other reactions. Reaction *b* is a compound one. There is evident flexor augmentation during double stimulation. This is accompanied by extensor contraction. Reaction *c* is a "pure" extension-reflex obtained with a slightly stronger strength of stimulation than that used in *b*. In extent, however, it is very similar to a former "pure" extension-reflex taken at the same strength as that used in *b*.

Reaction *k* is another compound one in which the contralateral stimulus used is considerably stronger. Evident flexor augmentation occurs during double stimulation, but there is no extensor contraction. Immediately after this a "pure" contralateral reaction was recorded at this strength of stimulus (reproduced in 7, fig. 30). This was an extension-reflex of "decerebrate" form. But 5 minutes before recording reaction *a* in this figure the same stimulus gave an abnormal flexion-reflex (7, fig. 29).

Between reactions *c* and *k* there were recorded six reactions which have previously been reproduced (6, fig. 3).

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and was equivalent in value to the extent of flexor contraction conditioned by the application of an ipsilateral stimulus during the period of application of a contralateral. In such cases this augmentation of flexor contraction seems to be the equivalent of the more than complete relaxation of extensor contraction which is conditioned by the subsequent application of a flexion-producing stimulus during the period of an extension-producing stimulus.

But in other cases an extensor contraction may accompany the augmented flexor contraction which is conditioned by the application of an extension-stimulus during the application of a flexion-stimulus. The flexor augmentation and the extensor contraction may then last throughout the period of the compounded stimuli. The extent of flexor contraction during the period of double stimulation is then greater than in the "pure" flexion-reflex evoked by the ipsilateral stimulus alone. The extent of the extensor contraction is, however, considerably smaller than in the "pure" extension-reflex. In an instance of this nature the "pure" contralateral stimulus evoked at one period in the experiment an abnormal crossed flexion-reflex (7, fig. 29). Ten minutes later it evoked a reaction of pure extension. When the contralateral stimulus was applied during the application of an ipsilateral stimulus there was a marked augmentation of the flexor contraction, and at the same time there was an extensor contraction which persisted during the period of double stimulation but was not of so great extent as that of the "pure" extension-reflex. The strength of ipsilateral stimulation was then kept constant, but that of the contralateral stimulus was gradually increased in a series of successive compounded reactions. As the strength of contralateral stimulation was increased there appeared to be an increase in the extent of flexor augmentation and a decrease in the extent of extensor contraction. Finally, the flexor augmentation became maximal and at this point no extensor contraction appeared during the period of double stimulation, but there was only extensor relaxation which brought the extensor curve in the record below the level of rest (fig. 10). This increase of the flexor augmentation during double stimulation with increase in the strength of the interrupting contralateral stimulus is probably related to the increase of the flexion factor of the "decerebrate" type of contralateral extension-reflex which is seen when, in series of "pure" reactions, the strength of the contralateral stimulus is progressively increased.

Occasionally it occurs that there may be a flexor augmentation in the first part of the period of double stimulation, but that there is a subsequent flexor depression while the two antagonistic stimuli are still compounded. This effect may be seen when the two stimuli are commenced and terminated synchronously. The flexor contraction is then at first greater than in the "pure" flexion-reflex, but soon becomes considerably smaller. In an experiment of this type a contralateral stimulus was compounded with an ipsilateral—both being of constant strength in a series of reactions in which the interval between the commencement of the ipsilateral flexion-producing

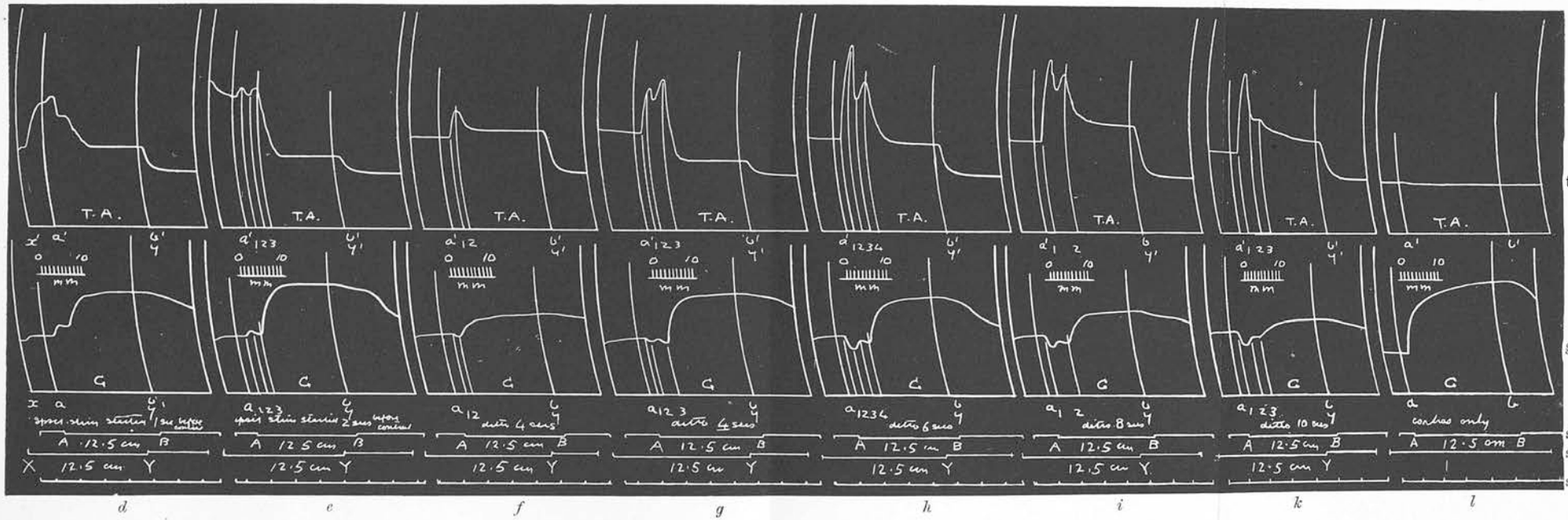


FIG. 11.—Experiment C, xxxiii., record 58, 1563; 10/4/11.—Decerebrate cat. A series of reactions obtained 3 hours and 20 minutes after decerebration. This series directly follows that reproduced in fig. 2—1-minute interval between the last reaction (*c*) in that figure and the first in this (*d*). Here there are 2-minute intervals between the reactions, save between *f* and *g*, where the interval is one of 3 minutes. Reaction *f* was immediately preceded by a similar but unrecorded reaction, which may have "fatigued" the preparation.

Reaction is a "pure" extension-reflex; compare with reaction *a* in fig. 2, which is taken at the same strength of stimulation.

In the other reactions the contralateral stimulus is applied at ever greater intervals of time after the commencement of the ipsilateral. The first part of each ipsilateral reaction is not recorded. The intervals between the two stimuli are 1, 2, 4, 4 seconds (again), 6, 8, and 10 seconds in reactions *d*–*k*. Note the flexor augmentation at its maximum in reaction *h*, and the extensor contraction during double stimulation at its maximum in reaction *e*. This series demonstrates flexor augmentation during double stimulation when the contralateral stimulus if applied "pure" gives extensor contraction alone.

stimulus and that of the contralateral extension-producing stimulus was progressively lengthened (fig. 11). When the second stimulus (extension) was added to the first there was at first a period of 1–1·5 seconds in which there was augmentation of flexor contraction, and in which there was no extensor contraction. The period of double stimulation was about four seconds in each case, and the remaining 3–2·5 seconds were occupied by a phase of flexor relaxation and extensor contraction. The flexor relaxation not only brought the curve of the flexor muscle down to the extent of the "pure" flexion-reflex, but reduced it considerably below that level. Starting with a small interval of time (one second) between the commencement of the ipsilateral stimulus and that of the contralateral, there was a comparatively small amount of flexor augmentation, and the subsequent flexor relaxation was great in extent. At the same time the extensor contraction was present in the second phase of the compounded reaction. (When both the stimuli were commenced at the same time the initial flexor augmentation was greater; the following flexor relaxation was not so great; and the extensor contraction which accompanied the phase of flexor relaxation was also not so great as in the reaction in which there was a short interval of time between the two commencements: the extensor contraction was considerably smaller than in the "pure" extension-reflex.) As the interval between the commencement of the two stimuli was then progressively lengthened—interval 1, 2, 4, 6, 8 and 10 seconds—the flexor augmentation gradually increased in value until a maximum was reached when the interval between the commencement of the ipsilateral and of the contralateral stimulus was six seconds. The following flexor relaxation shewed its greatest relaxation when the interval was four seconds. The extensor contraction at the interval of two seconds was at its greatest and then appeared to be greater than that of the "pure" extension-reflex. Thereafter it gradually diminished in extent. After the maximum of flexor augmentation had been reached it gradually decreased with progressive lengthening of the interval between the commencements of the two stimuli. At the same time the amount of the following flexor relaxation gradually diminished. At the end of the series, when the two stimuli were compounded after the ipsilateral flexion-producing stimulus had been in application for ten seconds, there still was marked—although diminished—flexor augmentation; the following flexor relaxation was small—so that actually there was a persisting flexor augmentation throughout the period of double stimulation; and the extensor contraction was small. A subsequent "pure" extension-reflex (2 minutes after the end of the series), exhibited an extensor contraction greater than at the beginning of the series. A repetition of this series gave somewhat similar results, but the extensor contraction was never so great as in the "pure" extension-reflex (fig. 11) [see also xvii., figs. 4, 5, 6, and 14].

It may also happen that where the extension-reflex is of "decerebrate" type—without actually exhibiting a flexor element of contraction,—if it is compounded against a subminimal background of flexion, such a flexor

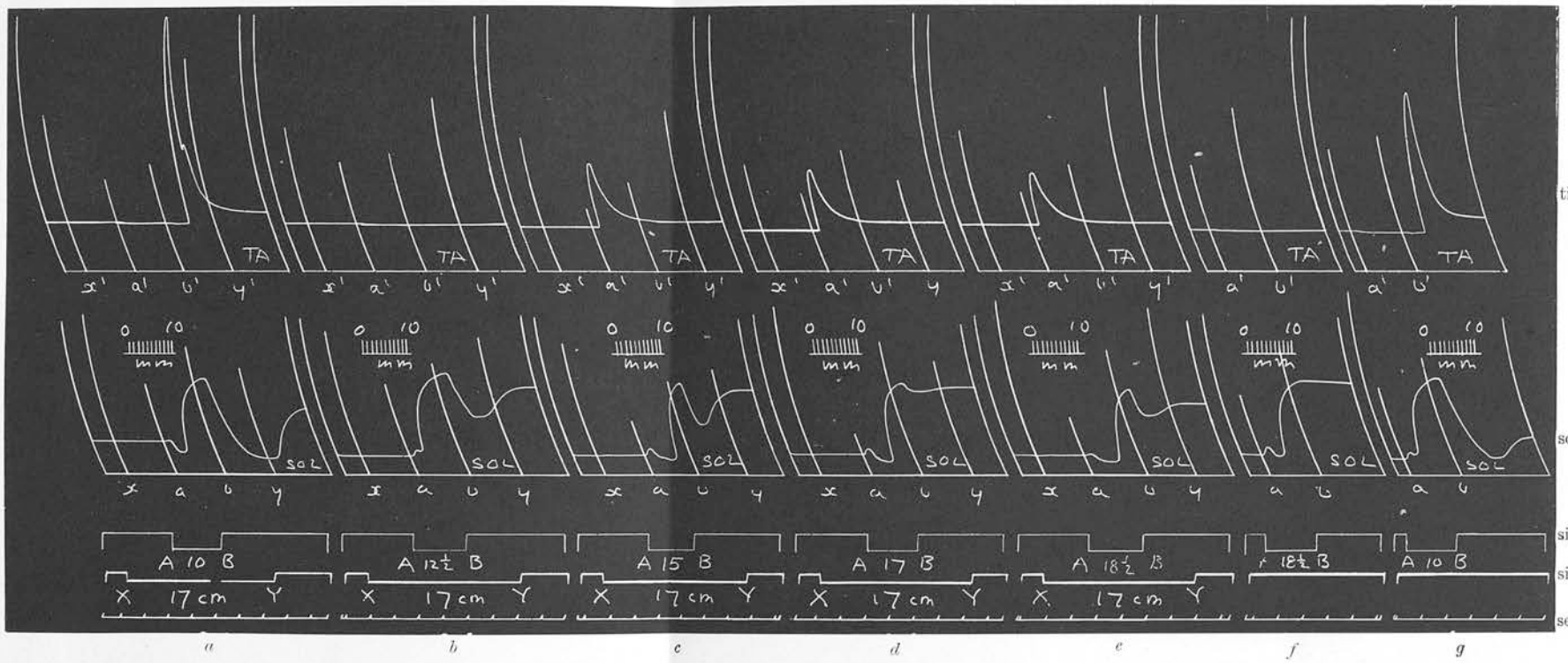


FIG. 12.—Experiment C, clxviii., record 299, 7715; 27/2/13.—Decerebrate cat. A series of compound reactions obtained 4 hours and 54 minutes after decerebration—minute intervals. Note that the extensor here used is the soleus component of gastrocnemius-soleus.

Reaction *g* is a "pure" extension-reflex of the same strength and duration of stimulation as that used in the compound reaction *a*. Note the "decerebrate" type of reaction, the terminal extensor relaxation, and the reciprocal "flexor rebound contraction after inhibition." The extensor relaxation is followed by a later extensor rebound contraction.

Reaction *f* is a "pure" extension-reflex taken with a weaker stimulus of the same strength as that used in compound reaction *e*. Note here the absence of any terminal phenomenon except the extensor after-discharge.

Reactions *a*–*e* are compound. The ipsilateral "background" is subliminal, and the strengths of the contralateral stimuli are progressively reduced. In the phases of double stimulation there is a preliminary flexion factor—extensor relaxation and flexor contraction. This is better marked the weaker the contralateral stimulus [the reverse of this is the more usual occurrence, as it is also in series of "pure" extension-reflexes of "decerebrate" type]. In the fourth phases (ordinates *b*, *b'*; *y*, *y'*) of the compound reactions there is extensor relaxation (accompanied by reciprocal flexor contraction in *a*). This is of less extent the weaker the contralateral stimulus. In every case the extensor relaxation passes over into contraction again, and this is continued as an extensor after-discharge in the fourth phases of the compound reactions. In *a* the extensor restitution of contraction occurs in the fourth phase alone. In the other reactions it commences in the third phases.

On comparison of reactions *a* with *g* and *e* with *f* it is seen in the first place that there is an exaggeration, in the phase of double stimulation, of the flexion element in the corresponding "pure" extension-reflex. In *e* this takes the form of the appearance of flexor contraction. It here appears as if the subliminal ipsilateral flexion "background" tended to exaggerate the factor of flexion in the extension-reflex.

Secondly, it will be observed that the flexor contraction in the third phase of *a* is of greater extent than is the flexor rebound contraction in *g*—the corresponding "pure" extension-reflex; and that—on comparison of *e* and *f*—where there is no extensor terminal relaxation in the corresponding "pure" extension-reflex there may yet appear extensor relaxation in the third phase of the compound reaction. It therefore looks as if the presence of a subliminal flexion "background" also exaggerates the flexion factor in the terminal phenomena of the extension-reflex—and may even cause that to appear when not evidenced in the "pure" reaction.

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element may appear (fig. 12). As the ipsilateral stimulus is subminimal, in such a case the reaction during the phase of double stimulation has the same appearance as the "pure" extension-reflex—save that the element of extensor relaxation, which occurs near the commencement of the reaction of "decerebrate" type, is exaggerated in extent and duration, and that a reciprocal element of flexor contraction (not present in the "pure" reaction) is added.

Where the results of the compounding of two antagonistic stimuli have been of the ordinary form—partial flexor relaxation and partial extensor contraction—the reactions have also been examined in such series.

In these instances it is found that when the contralateral extension-producing stimulus is increased in strength relatively to the ipsilateral flexion-producing stimulus, the extent of the flexor relaxation conditioned by the application of the contralateral stimulus during the period of ipsilateral stimulation is increased, and so too is the extent of the concomitant extensor contraction. If the relative strength of the contralateral extension-producing stimulus be reduced, then the effect of flexor relaxation and extensor contraction in the compounded reaction is diminished.

When the two antagonistic stimuli of the compounded reaction are kept of constant value but their temporal relationships changed, it is found that, as in the low spinal preparation, there may be a change in the form of the reaction. In general this is such that the later after the commencement of the ipsilateral flexion-producing stimulus the contralateral stimulus is first applied the greater is the effect of flexor relaxation and of extensor contraction (see xvii. figs. 1, 2, and 15).

## VI. On the Influence of the Kind of Preceding Stimulus upon the Phenomena during Double Stimulation.

In the immediately preceding paper of this series it was observed that in the low spinal preparation the algebraic summation which is conditioned by the compounding of two stimuli differs in value according as either the contralateral (extension-producing) or the ipsilateral (flexion-producing) stimulus is commenced before the period of double stimulation. Thus, with stimuli the strengths of which are unchanged, if one is commenced two seconds before the period of double stimulation the phenomena during that period are not quite similar to those which are obtained if the other stimulus is first applied and also commenced two seconds before the period of double stimulation. Similar differences are seen in the decerebrate preparation.

In previous sections of this paper it has been shewn that the phenomena during double stimulation vary with variation in the duration of the stimulus first applied, and that usually this variation is such that the longer the first applied stimulus is allowed to run before the application of the other, the greater is the component conditioned by the second stimulus

in double stimulation. In other words, when a stimulus is applied and allowed to run on, upon the whole the centres become more predisposed towards an opposite activity the longer the stimulus has been in being.

If therefore we were to take two antagonistic responses, $\Sigma$ and $\sigma$, the evocative stimuli of which when applied together give an algebraic summation of flexion ($\Sigma$) and extension ($\sigma$), the value of this summation might be expected to vary according to whichever of the two stimuli "held the field" at the commencement of double stimulation. We may suppose that the first stimulus to be applied is allowed to run for two seconds before the addition of the second. When the second stimulus is applied the value of the response of the first will have deteriorated relatively to its value at the commencement of the first two seconds of "pure" stimulation. This deteriorated value may be denoted by the sign $\Sigma'$ or $\sigma'$, as the case may be; and these are such that $\Sigma > \Sigma'$ and $\sigma > \sigma'$. Now, if both the stimuli are commenced at the same time the value of the summation of their responses may be denoted by the symbols $\Sigma + \sigma$. But if the flexion-producing stimulus be commenced before the commencement of the extension-producing the value of the summation will be $\Sigma' + \sigma$, whereas if the extension-producing stimulus be first applied the value of the summation will be $\Sigma + \sigma'$. But, as $\Sigma > \Sigma'$ and $\sigma > \sigma'$, these three different values of summation will be such that $[\Sigma + \sigma'] > [\Sigma + \sigma] > [\Sigma' + \sigma]$ as regards the component of flexion in the summation, and $[\Sigma + \sigma'] < [\Sigma + \sigma] < [\Sigma' + \sigma]$ as regards the component of extension in the summation.

Thus where the two stimuli used are applied in the same temporal arrangement, but in one instance the flexion-producing stimulus is first applied and in the other the extension-producing stimulus is first applied, it would be expected that there would be a greater degree of extension in the compound phenomenon during double stimulation when the flexion-producing stimulus is first applied, and a greater degree of flexion in that phenomenon when the extension-producing stimulus is first applied.

In these experiments the first stimulus to be applied usually was allowed to run for two seconds only before the addition of the second stimulus, and under these conditions the above-mentioned relationship of the flexion and extension factors in double stimulation occurs but rarely (fig. 13). In such an instance the level of flexor contraction during double stimulation is greater when the ipsilateral (flexion-producing) stimulus is added to the contralateral, when that has run for two seconds, than when the contralateral is added to the ipsilateral after that has been running for two seconds. At the same time, the level of extensor contraction during double stimulation is greater in the latter case than in the former. This has been observed to occur when the contralateral stimulus was comparatively strong—as estimated by the extent of the extensor contraction in the "pure" extension-reflex—and when the ipsilateral reaction (of "decerebrate" type) was comparatively weak.

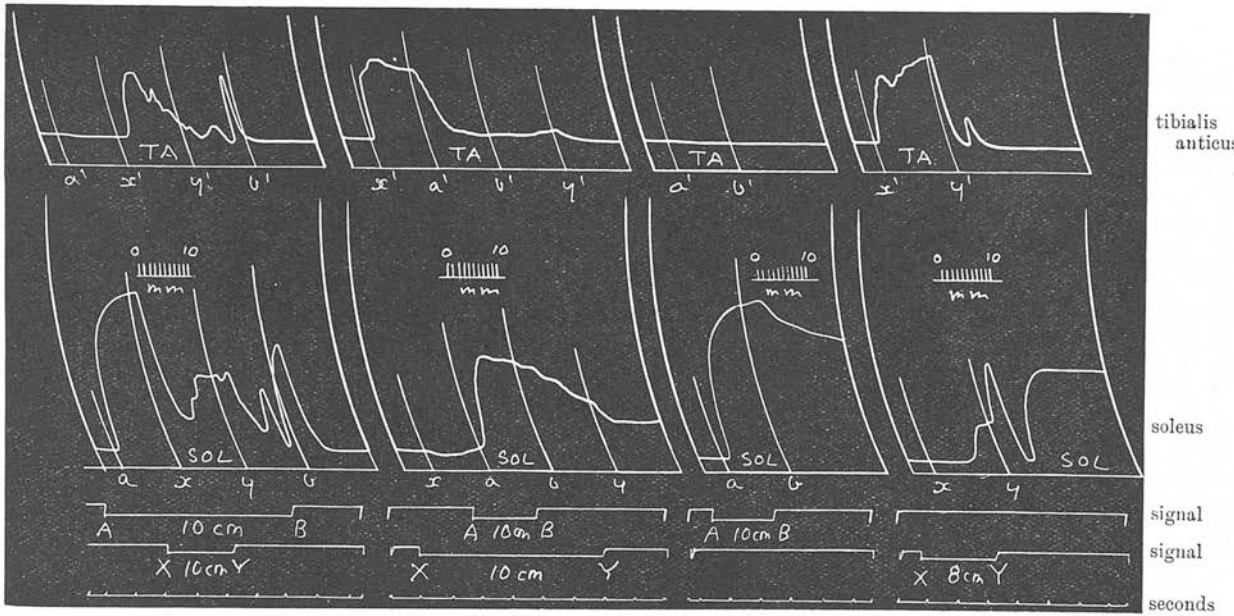


FIG. 13.—Experiment C, cliii., record 276, 6553; 9/1/13.—Decerebrate cat (the extensor here is soleus alone). A series of reactions obtained 4 hours and 2 minutes after decerebration.

Reaction *c* is a "pure" extension-reflex—note the extensor after-discharge. Reaction *d* is a "pure" ipsilateral flexion-reflex of "decerebrate" type. (Note that the late extensor contraction during ipsilateral stimulation may therefore occur in soleus which has no flexion action at any joint.) Note the extensor rebound contraction which is followed by relaxation and a reciprocal flexor rebound contraction, and finally by a maintained tonic extensor contraction. The ipsilateral stimulus used in *d* is somewhat stronger than that used in *a* and *b*.

In reaction *a* the contralateral stimulus is first applied, and then the ipsilateral. During the period of double stimulation ($x$, $x'$–$y$, $y'$) there is a flexor contraction which is less than in the "pure" flexion-reflex, and an extensor relaxation. This relaxation again gives place to increasing contraction as the period of double stimulation is continued. Note the irregular rhythmic phenomena in the period which succeeds that of double stimulation. An extensor after-discharge is not present.

In reaction *b* the two stimuli are applied in a reversed temporal arrangement. Here during double stimulation ($a$,$a'$–$b$,$b'$) the flexor relaxes almost completely, so that at the end of the period of double stimulation its level of contraction is lower than in reaction *a*. At the same time the extensor contracts and its level of contraction—while less than in the "pure" extension-reflex—is greater than the level of extensor contraction in the period of double stimulation of reaction *a*. Note here a depression of the extensor after-discharge.

It has been found—when the interval of time between the commencement of the two antagonistic stimuli is of about two seconds' duration—that it is far more common for the extension to be greater during double stimulation when the contralateral stimulus is first applied, and reciprocally

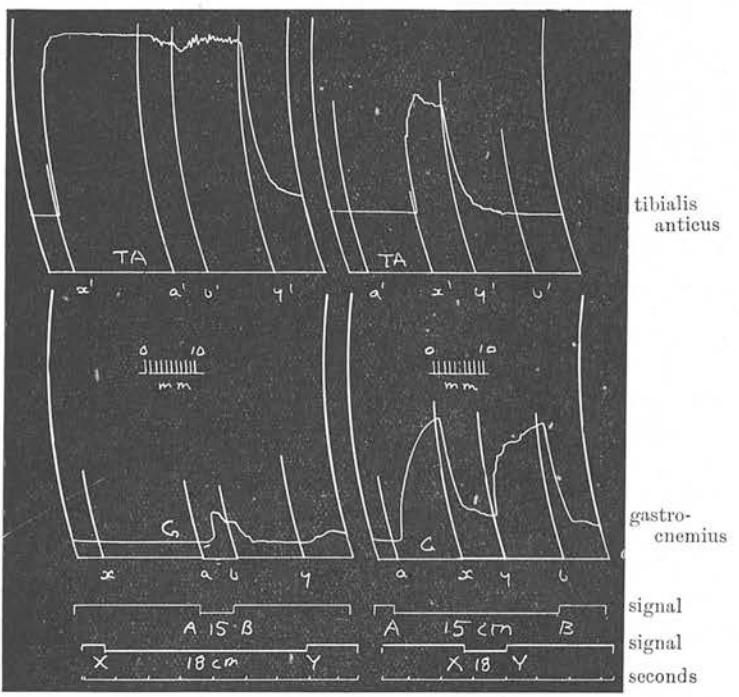


FIG. 14.—Experiment C, clxiii., record 261, 6133; 2/11/12.—Decerebrate cat. Two reactions obtained 1 hour and 57 minutes after decerebration—an interval of 1 minute between them.

In reaction *a* the ipsilateral stimulus is first applied, and after an interval of about 3 seconds the contralateral is commenced. The period of double stimulation is one of about 1 second in duration. Note the relatively slight flexor relaxation and extensor contraction during double stimulation.

In reaction *b* the contralateral stimulus is first applied, and then, after an interval of about 2 seconds, the ipsilateral stimulus is commenced—the period of double stimulation here being about 1·3 seconds. Note that the flexor does not rise to the same level of shortening which obtained during the period of double stimulation in reaction *a*, and that the extensor relaxes to a level which is higher than the level of contraction in the double stimulation of *a*. Note also the sudden extensor relaxation on withdrawal of the contralateral "background" stimulus. In a "pure" contralateral reaction taken 1 minute before *a* with the same strength of stimulation, but with a duration of 2 seconds only, there was a well-sustained extensor "tonic" after-discharge.

for the flexion to be less, than when the ipsilateral stimulus is first applied (figs. 14, 15). In such cases, if the contralateral stimulus be applied during the running of the ipsilateral, the extensor contraction during double stimulation may be almost absent, and there may be comparatively little flexor relaxation; yet in the double stimulation produced when the contralateral stimulus is first applied there may be a flexor contraction which

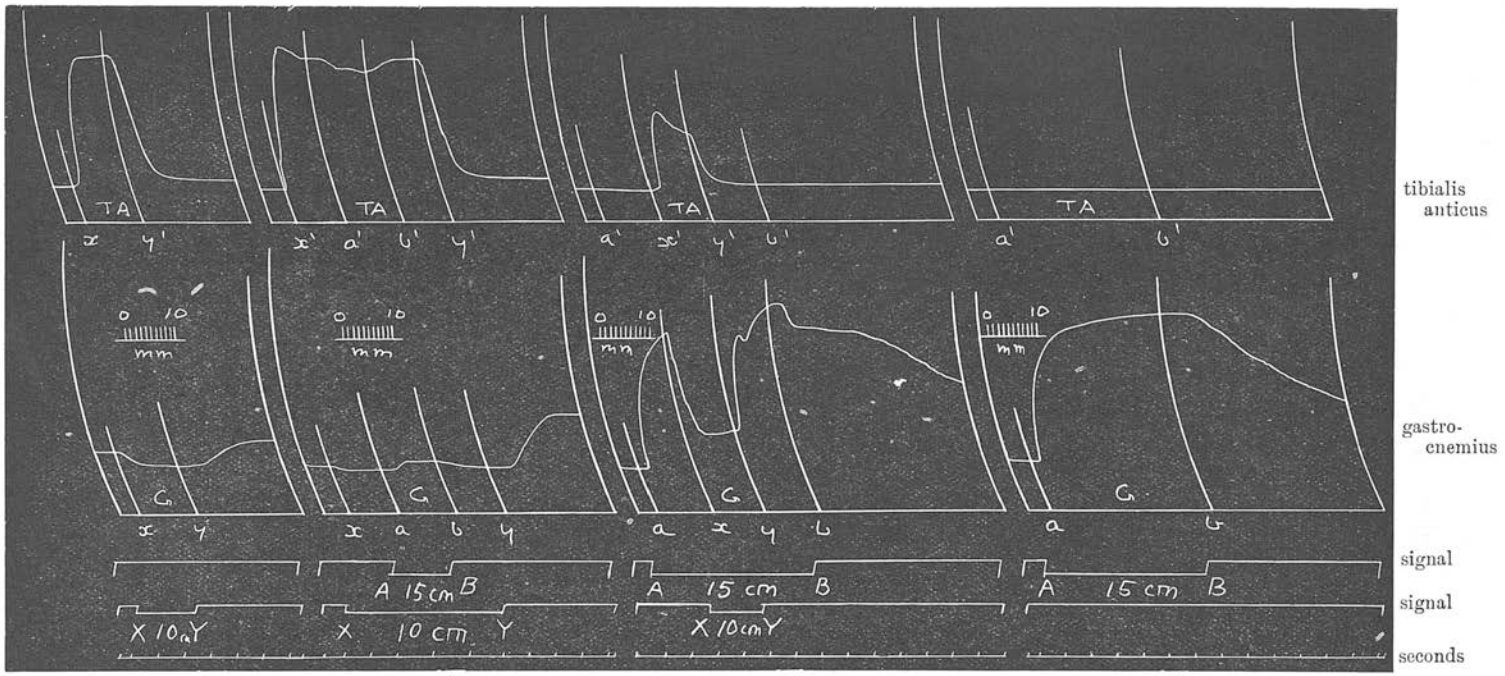


FIG. 15.—Experiment C, clv., record 278, 6597; 30/1/13.—Decerebrate cat. A series of reactions obtained 2 hours and 38 minutes after decerebration, and taken at minute intervals.

Reaction *a* is a "pure" flexion-reflex—note the tonic extensor rebound contraction.

Reaction *d* is a "pure" extension-reflex—note the extensor after-discharge.

In reaction *b* the ipsilateral stimulus is first applied, and then, after about 2 seconds, the contralateral stimulus is added—the period of double stimulation lasting about 2 seconds. There is very slight flexor relaxation and extensor contraction during double stimulation; note the extensor tonic rebound contraction on final withdrawal of the ipsilateral stimulus. It is larger than in the "pure" flexion-reflex.

In reaction *c* the contralateral stimulus is first applied, and then, after about 2 seconds, the ipsilateral is added. Here the flexor does not attain to the level of contraction held during double stimulation in *b*; and the relaxation of the extensor is not down to the level of contraction attained in *b*.

In these two reactions (*b* and *c*), it will be observed that the extensor rebound is augmented in *b*, and that in the "third phase" of reaction *c* ($y,y' - b,b'$) there is an augmentation of the extensor contraction to a level greater than that which obtains in the corresponding period of the "pure" extension-reflex (reaction *d*). Compare this with the following figure.

does not attain to the level which the flexor took during the former double stimulation, and the extensor may relax only partially (figs. 14, 15).

Where the ipsilateral stimulus is comparatively strong there may be no extensor contraction during double stimulation when the ipsilateral stimulus is first applied, and complete extensor relaxation during double stimulation when the contralateral stimulus is the "background"; but nevertheless, although there may be no flexor relaxation during double stimulation in the former case, there may be an incomplete flexor contraction during double stimulation in the latter case (fig. 16).

In these experiments, in a few instances the relative effects of double stimulation after preceding "backgrounds" of extension and of flexion have been examined in series of reactions in which one of the stimuli has been changed in strength.

In one of these instances the strength of the ipsilateral (flexion) stimulus was kept constant and compounded with two different strengths of contralateral (extension) stimulation—one of these being weak, and the other strong. It was then found that when the contralateral stimulus was weak the flexion element in double stimulation was actually greater when double stimulation was preceded by a "background" of extension than when preceded by a background of flexion, and the extension element was less. When the contralateral stimulus was strong the flexion element in double stimulation was smaller when the preceding background was one of extension than when it was one of flexion; and the extension was greater when the preceding background was one of flexion than when it was one of extension.

In another instance (figs. 24, 25, and xvi. fig. 16), with a constant contralateral stimulus a long series of reactions in which the ipsilateral stimulus was increased in strength was taken. At each strength of ipsilateral stimulation the effects were observed against flexion and extension "backgrounds." It was there found that when the ipsilateral stimulus was weak, the level of extensor contraction during double stimulation was smaller when the contralateral stimulus preceded it than when the ipsilateral did—that is, when the "background" was extension than when it was flexion. At a certain intermediate strength of ipsilateral stimulation the level of extensor contraction was about the same in the two cases; while with stronger ipsilateral stimuli the level of extensor contraction during double stimulation was smaller when the ipsilateral stimulus was first applied (flexion "background") than when the contralateral stimulus was (extension "background").

In this same experiment the ipsilateral stimulus was then kept at a certain comparatively weak strength, and the strength of the contralateral stimulus was varied. It was there found (fig. 26, and xvi. fig. 18) that at all strengths of contralateral stimulation the level of extensor contraction during double stimulation was greater when the preceding "background" stimulus was the ipsilateral (flexion) than when it was the contralateral

(extension), but that this relative difference was greater the stronger the contralateral stimulus was.

These experiments seem to shew that, to a certain extent, the first

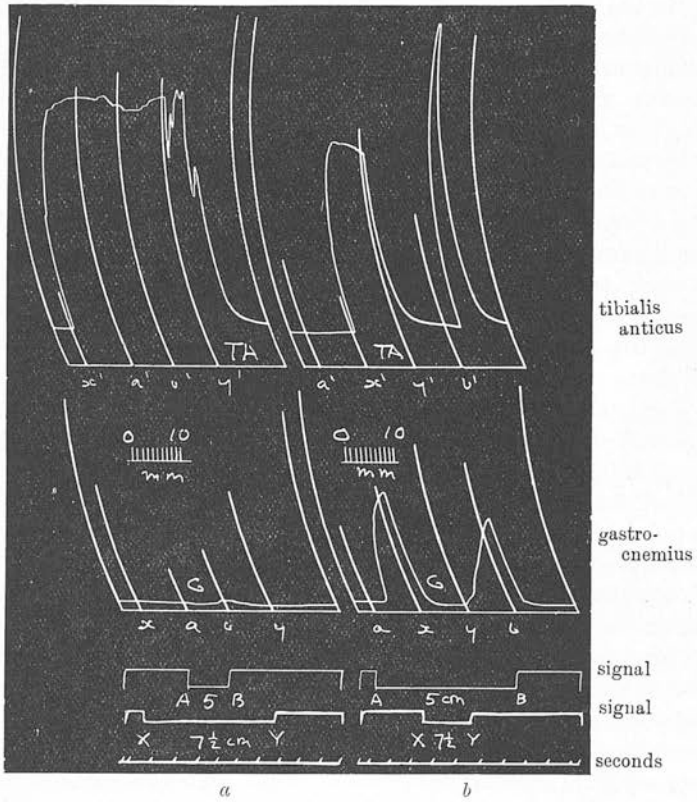


Fig. 16.—Experiment C, clxxiii., record 306, 8075; 10/3/13.—Decerebrate cat. Two reactions obtained 3 hours and 17 minutes after decerebration and taken at minute intervals. A reaction taken 1 minute previously (not reproduced), and in response to a "pure" ipsilateral stimulus, gave a very slight extensor rebound contraction of maintained form and somewhat similar to that reproduced in the previous figure. In a "pure" extension-reflex there was an extensor after-discharge.

In reaction *a* the ipsilateral stimulus is the "background." Double stimulation is unaccompanied by any noticeable flexor relaxation, and there seems to be an extensor relaxation. The flexor after-discharge which is here present was not present in a previous "pure" flexion-reflex, which, however, was one of 2 seconds' duration only.

In reaction *b* the "background" is one of extension. Note that here during double stimulation there is complete extensor relaxation, but that still the flexor does not attain to the level of contraction held during double stimulation in reaction *a*.

Note that in the third phase ($y,y' - b,b'$) of reaction *b* there is depression of extension, and that the cessation of the contralateral stimulus is not here followed by an extensor after-discharge, but that there is a flexor rebound contraction not present in the "pure" extension-reflex. These phenomena are the opposite of those present in the previous figure; but yet the phenomena during double stimulation in the two figures are comparable.

stimulus to be applied "holds the field," so that the activity it evokes plays a greater part in a compound reaction produced by the subsequent application of an antagonistic stimulus while the first is still running. But the

strength of this capture of the field seems to fade as the first applied stimulus is continued, so that the later the second stimulus is applied the greater part does the specific activity (flexion or extension) evoked by it play in the compound phenomenon. But the experiments also seem to shew that not only may this "capture of the field" fade away, but that it may actually reverse—so that in these circumstances the activity of the second stimulus may play a greater part in the compound phenomenon than when it is the "background" stimulus and the other is the "interruptor."

In other words, these experiments seem to demonstrate that when a stimulus and its evoked reaction are weak the field is held for a shorter space of time than when they are strong, and that this capture of the field may actually reverse within the short space of two seconds when the stimuli used are very weak. This phenomenon is almost certainly allied to the late extensor contraction observed in the "decerebrate" types of flexion-reflex, and to the abnormal extension response observed in some cases when weak ipsilateral stimuli are used.

Further to test this point, some series of reactions, in which the strengths of stimuli have been constant but their time-relations varied, have been recorded. In these cases the method has been to take a series in which the ipsilateral is the "background" stimulus and vary the duration up to the point of double stimulation of the first applied stimulus, and then to do the same when the contralateral stimulus is the "background" (compare xvi. fig. 8 with xvii. fig. 2 [where, however, the strengths of contralateral stimulation are slightly different], and xvi. fig. 21 with xvi. fig. 15).

One such instance may be quoted (see xvi. fig. 21 and xvii. fig. 15). Here the time intervals selected were 0 seconds (synchronous commencement of the antagonistic stimuli), 2 seconds, and 4 seconds. With synchronous commencement of the two stimuli there was almost complete suppression of the extensor contraction. In every case double stimulation lasted for two seconds, and here there was a slight extensor contraction during the last second of the period of double stimulation. When the interval between the commencement of the first stimulus to be applied and the commencement of double stimulation was two seconds, and when the "background" was one of flexion, there was a good extensor contraction which commenced early in the period of double stimulation and a good reciprocal flexor relaxation. With a flexion "background" the level of extensor contraction during double stimulation was lower and that of flexor contraction was higher than in the former case (flexion "background"). The differences between these heights of the level of contraction were about 5 mm. (extensor), and about 13 mm. (flexor)—as measured just before the termination of the two seconds of double stimulation.

When the time which elapsed between the commencement of the "background" stimulus and the commencement of double stimulation was four seconds, it was found, against the flexion "background," that the level of extensor contraction during double stimulation was about 6 mm. higher

than the level of extensor contraction during double stimulation when the "background" was one of extension; while at the same time the level of flexor contraction during double stimulation was about 12 mm. lower than in the latter case.

In this experiment the effect of double stimulation of one second only in duration was also examined when the preceding "backgrounds" were of one second duration also. Here with a flexion "background" the extensor contraction was 2·5 mm. smaller than the extensor contraction when the "background" was extension. The figures as they concern the extensor alone (measured at the end of the first second of double stimulation) may be given in the following table[1]:—

Height of Extensor Contraction in mm.

| Duration of "background" . . | 0 sec. | 1 sec. | 2 sec. | 4 sec. |
|---|---|---|---|---|
| Flexion "background" . . . | [0 mm.] | 11 mm. | 13 mm. | 18 mm. |
| Extension "background" . . | [0 mm.] | 14 mm. | 13 mm. | 13·5 mm. |
| Difference of flexion "background" as against extension | ... | −3 mm. | 0 mm. | +4·5 mm. |

Thus with a very brief previous duration of the "background" stimulus there may be a greater extensor contraction at the end of the first second of double stimulation when the extension stimulus is first applied than when the flexion stimulus is; with a longer previous duration of the "background" the extensor contraction may be about the same in the two instances; and with a still greater previous duration of the "background" stimulus there may be a smaller extensor contraction with an extension than with a flexion "background."

Thus upon the whole it may be said that when a flexion "background" is under consideration flexion activity in the early phases "holds the field," but that this wears off—so that an extension stimulus will have an ever greater effect the later it is added. And it may also be said that the same holds good for a flexion stimulus against an extension "background"—with this reservation, that often the flexion effect of the ipsilateral stimulus in double stimulation is greatest (or at any rate very great) when the two stimuli are commenced synchronously—that is, when there is no preceding "background." The explanation of this probably lies in the presence of a preliminary tendency to flexion activity in the extension-reflex, as evidenced in such phenomena as the "decerebrate" type of that reaction. If it be the case that in the extension-reflex there is a preliminary factor

[1] The figures in the text differ from those in the table because the former refer to the state of the muscles at the end of the second second of double stimulation, while the latter refer to that state at the end of the first second of double stimulation. In both cases the figures are directly proportional to, but are not equal to, the shortening of the muscle in contraction.

of flexion, it is not difficult to suppose that in the compounding of activities during double stimulation there may be summation of the two flexion factors—namely, those of the flexion-reflex and of the flexion factor in the crossed extension-reflex.

If it be admitted that the value of a reflex activity changes during the continuation of the evoking stimulus (reflex "fatigue"?), the change may be formulated thus: $\Sigma > \Sigma' > \Sigma'' > \Sigma'''>$, etc., for ipsilateral flexion, and $\sigma > \sigma' > \sigma'' > \sigma'''>$, etc., for contralateral extension. Taking the series $\Sigma$, $\Sigma'$, etc., double stimulation at any one point may be represented by $\Sigma+\sigma$, $\Sigma'+\sigma$, $\Sigma''+\sigma$, $\Sigma'''+\sigma$, etc., where $\sigma$ is constant. And, taking the series $\sigma$, $\sigma'$, etc., double stimulation may be represented by $\sigma+\Sigma$, $\sigma'+\Sigma$, $\sigma''+\Sigma$, $\sigma'''+\Sigma$, etc., where $\Sigma$ is constant. $\Sigma+\sigma=\sigma+\Sigma$ of course.

If one activity only be considered—let us take extension—these formulæ for the values of double stimulation are such that $[\Sigma'+\sigma]<[\sigma'+\Sigma]$ (duration of previous "backgrounds" small); $\Sigma''+\sigma=\sigma''+\Sigma$ (duration of previous "backgrounds" greater); and $[\Sigma'''+\sigma]>[\sigma'''+\Sigma]$ (duration of previous "backgrounds" yet greater).

These formulæ are only convenient modes of expressing the fact that there is a certain duration of previous "background" at which the value of double stimulation is the same whether the flexion-producing or the extension-producing stimulus be first applied; and that with "backgrounds" of a lesser duration the first evoked activity tends to "hold the field," while with "backgrounds" of greater duration the reverse is the case—so that the activity evoked by the stimulus which is superposed upon the "background" has a greater value than when that activity is the "background" itself. The neutral duration of "background" may be looked upon as a point of balance which perhaps is evidenced in all reflex activities.

## VII. Phenomena in Preparations which exhibit Abnormal Reactions.

### A. Ipsilateral Extension and Contralateral Extension.

Occasionally the ipsilateral reaction may be one of abnormal extension. This effect is most often seen with weak stimuli, and it changes over into a reaction of flexion as the strength of stimulus is increased. Sometimes, however, the ipsilateral reaction throughout an experiment may be one of extension to all strengths of stimuli used.

In this latter type of experiment summation of the factors of extension may occur when there is compounding of the ipsilateral and contralateral stimuli, both of which give extension reactions. In such a case the value of the ipsilateral stimulus may be successively increased in a series of reactions in which the value of the contralateral stimulus is kept constant. In a series of this nature it was found that when the contralateral stimulus was commenced one second after the commencement of

the ipsilateral there was an augmentation of the contraction of the extensor. The value of the augmented extensor contraction was, however, usually smaller than that of the extensor contraction in the "pure" extension-reflex; and this was most clearly seen when the strength of the ipsilateral stimulus was comparatively great. When the ipsilateral stimulus was commenced in time one second after the contralateral there was, with weak values of ipsilateral stimulation, augmentation of extensor contraction. This was of a degree greater than that of the "pure" extension-reflex. With stronger ipsilateral stimuli this augmentation was not seen, and there was even a very slight indication of extensor relaxation during the period of double stimulation—but this was too small to be clearly defined.

In another experiment (figs. 17, 18, 19) this relaxation phenomenon was more clearly seen. Here it was found that with weak ipsilateral and contralateral stimuli there was summation of the extension reactions during double stimulation (fig. 17), so that the extent of extensor contraction was there greater than in either "pure" reaction. When "pure" stimuli of greater strength were used the contralateral reaction was found to be of much greater extent of extensor contraction than the ipsilateral. During double stimulation the extent of extensor contraction was intermediate to the extents of the two "pure" reactions. Thus when the "background" reaction was contralateral extension there appeared extensor relaxation during double stimulation—but not down to the level of extensor contraction which obtained in the "pure" ipsilateral reflex (fig. 18). On the other hand, when the "background" was one of ipsilateral extension, during double stimulation there was augmentation of extensor contraction—but not to the level which obtained in the "pure" contralateral reflex (fig. 19). On comparison of the immediate effects of double stimulation against the two different "backgrounds" it was found here that the extent of extensor contraction after two seconds of double stimulation was greater when the "background" was one of contralateral extension.

In yet another, and a more recent, experiment a most curious example of this phenomenon was encountered. A "pure" ipsilateral reaction gave a good abnormal direct extension-reflex. A "pure" contralateral stimulus applied for six seconds gave an extension-reflex in which there occurred during stimulation a partial relaxation of extensor contraction, followed by restitution. The two stimuli were then compounded—"background" contralateral extension During double stimulation there was no summation of the two extensions. In the extensor curve there was complete relaxation; and this was accompanied in the flexor curve by a very marked flexor contraction. The ipsilateral stimulus was then repeated "pure," and gave a reaction which opened with extension and passed over into flexion during stimulation. In this instance, therefore, the presence of a "background" of contralateral extension reversed the effect of the

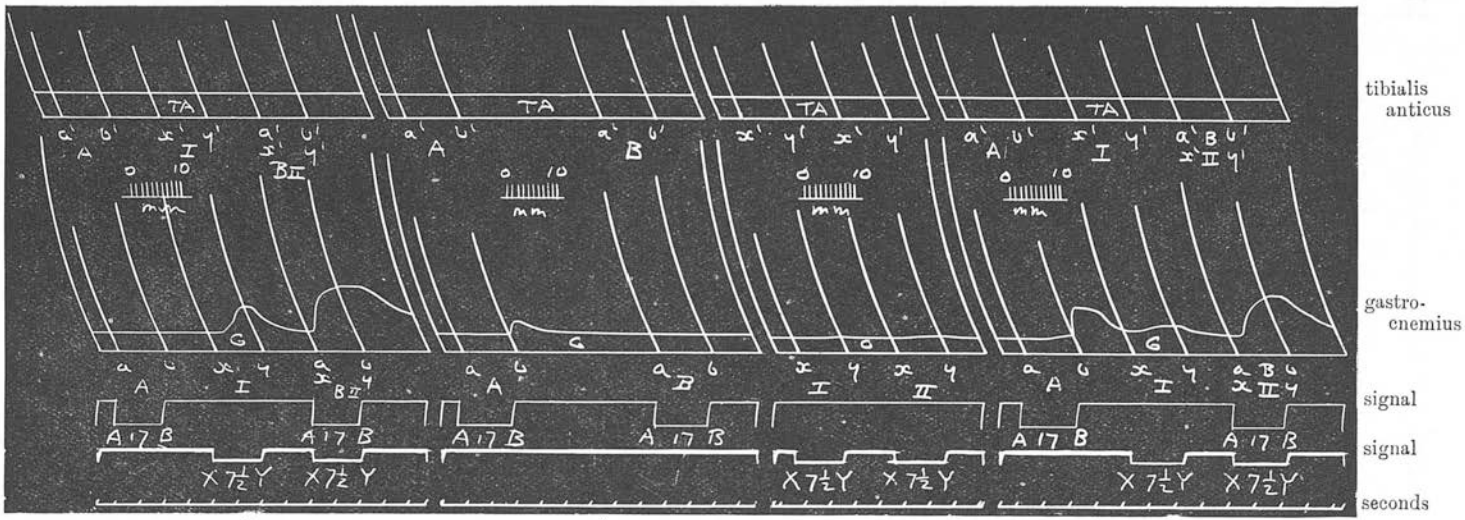


FIG. 17.—Experiment C, clxxii., record 305, 8012; 10/3/13.—A series of reactions obtained 2 hours and 42 minutes after decerebration; minute intervals.

In reaction *a* a subliminal contralateral stimulus is first applied "pure." After an interval of 2 seconds a liminal ipsilateral stimulus is applied, and evokes the abnormal reaction of ipsilateral extension. Two seconds later the two stimuli are applied synchronously. The resultant reaction is one of extension greater in extent than that of the "pure" ipsilateral reaction.

That this effect is not due to facilitation ("Bahnung") of either the contralateral or the ipsilateral effects used is demonstrated by the two following reactions.

Reaction *b* thus demonstrates the effect of repeating two contralateral stimuli of the same strength and at the same interval of time as in reaction *a*. The first stimulus at cessation is followed by an extensor rebound contraction—the second evokes no reaction either during or after stimulation. Therefore the effect is not due to facilitation of the contralateral reaction.

Reaction *c* repeats for the ipsilateral stimulus the arrangement of reaction *b*. Here the repetition of the ipsilateral stimuli at the same strength and time interval as in *a* obviously is not accompanied by facilitation of the second reaction. Therefore the effect is not due to facilitation of the ipsilateral reaction.

Reaction *d* is a repetition of reaction *a*. Here there is an extensor rebound contraction after the first contralateral stimulus, but with this exception the reaction is similar to *a*.

ipsilateral stimulus from one of abnormal extension to a strong flexion reaction (fig. 20).

In those experiments in which weak ipsilateral stimuli give the abnormal extension-reflex,[1] while stronger ipsilateral stimuli give the normal flexion-reflex, the results of the compounding of ipsilateral and contralateral stimuli are of interest.

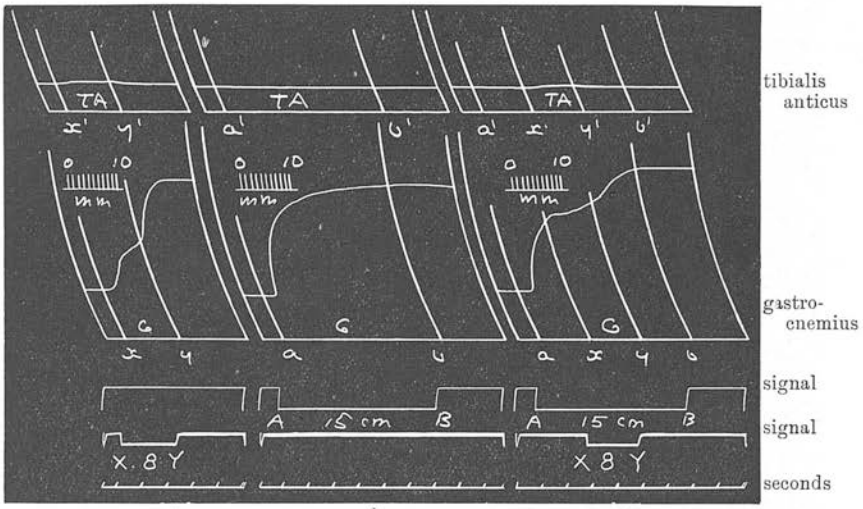


FIG. 18.—Experiment C, clxxii., record 305, 7999; 10/3/13.—Decerebrate cat. A series of three reactions obtained at minute intervals and 2 hours and 38 minutes after decerebration.

Reaction *a* is a "pure" ipsilateral reaction and demonstrates ipsilateral extension. Note the extensor rebound contraction after excitation.

Reaction *b* demonstrates a "pure" contralateral extension-reflex. Note the "tonic" extensor after-discharge.

In reaction *c* the two stimuli are compounded, the "background" being contralateral extension. During double stimulation there is evident extensor relaxation—or rather, the curve of increasing extensor contraction is retarded. Note that on withdrawal of the ipsilateral stimulus and when the contralateral is still running—that is, between ordinates *y*, *y'* and *b*, *b'*—the extensor contraction augments to a higher level than that attained during stimulation in the "pure" contralateral extension-reflex (*b*). This is also higher than the extensor rebound contraction in *a*. It looks here as if the extensor rebound contraction after the withdrawal of the ipsilateral stimulus can summate with the extensor contraction during stimulation of the contralateral reflex, but that the extensor contraction during stimulation of the ipsilateral reaction does not summate with the extensor contraction during stimulation of the contralateral reflex—a point of interest.

In an experiment of this nature the weak ipsilateral stimulus gave pure extension. A slightly stronger stimulus gave a preliminary flexor contraction followed by a marked phase of extension. A yet stronger ipsilateral stimulus gave flexion throughout the period of stimulation but

[1] I have of late, and for a special purpose, used preparations in which the operative procedure was carried out as rapidly as possible. Under these conditions a very large proportion of experiments demonstrate extension as a reaction to weak ipsilateral faradic stimuli. Weak mechanical stimulation of an ipsilateral afferent nerve may give the extension reaction, while strong mechanical stimulation may give the usual flexion-reflex.

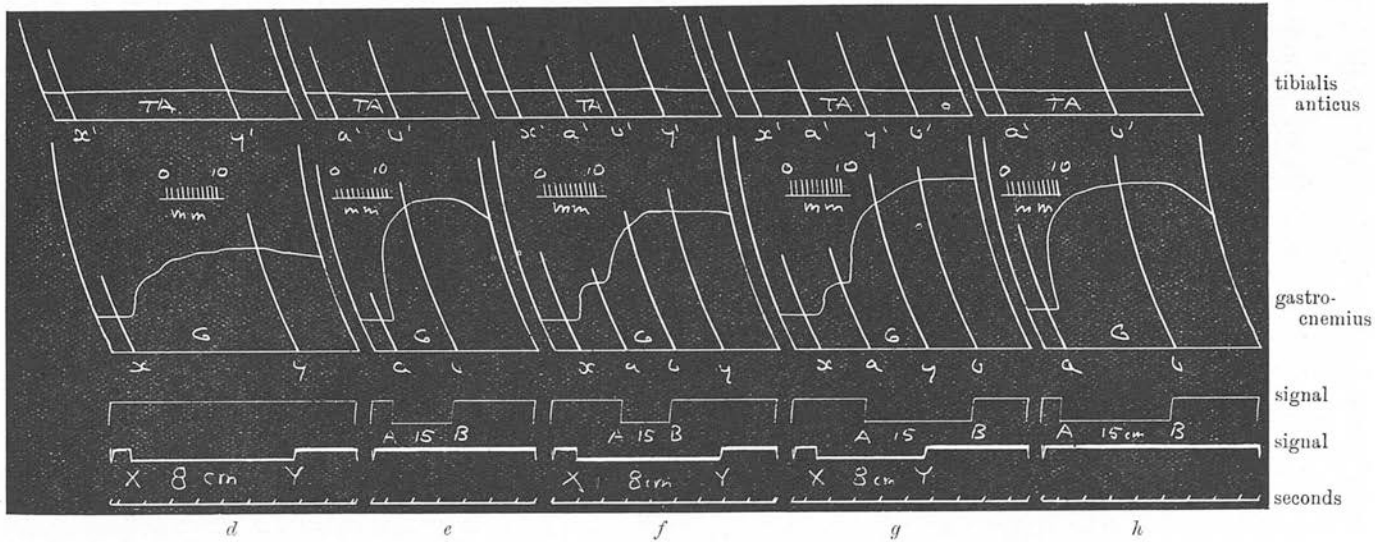


FIG. 19.—Experiment C, clxxii., record 305, 8002; 10/3/13.—Decerebrate cat. A series of four reactions taken at minute intervals, and 2 hours and 31 minutes after decerebration. Reaction *d* here follows reaction *c* of fig. 18 at an interval of 1 minute.

Reactions *d* and *e* are "pure" ipsilateral and contralateral reactions respectively.

In reaction *f* the two stimuli are compounded together—the "background" being one of ipsilateral extension. Here during double stimulation there is evident increase of extensor contraction, but the level of contraction attained is not so great as in the "pure" contralateral reaction (*e*). On withdrawal of the contralateral stimulus the extensor contraction continues to increase and then becomes level. There is therefore no relaxation down to the normal level of ipsilateral extensor contraction. On withdrawal of the ipsilateral stimulus there is no extensor rebound, but there is an extensor residual tonus.

Note that here, in *d*, there is no extensor rebound. (Compare with *a* in fig. 18—where the ipsilateral stimulus is applied for a shorter time.) Note also, in *f*, that the extent of extensor contraction during double stimulation is less than in reaction *c* of fig. 18—where the "background" is one of contralateral extension.

In reaction *g* a "step" arrangement of stimuli is used—the ipsilateral being first applied, then the contralateral, and then the ipsilateral stimulus being withdrawn during the application of the contralateral. Compare with *f*. Here on withdrawal of the ipsilateral stimulus there is a greater increase of extensor contraction than occurs in *f* on withdrawal of the contralateral stimulus. It is also greater than is the tonic extensor after-discharge of the contralateral reaction (*e* and *h*). Reaction *h* is another "pure" contralateral one in which the duration of contralateral stimulation is the same as in reaction *g*.

accompanied in the later phases of the period of stimulation by contraction of the extensor. Strong ipsilateral stimuli gave flexor contraction and extensor relaxation alone. The contralateral stimulus gave pure extensor contraction.

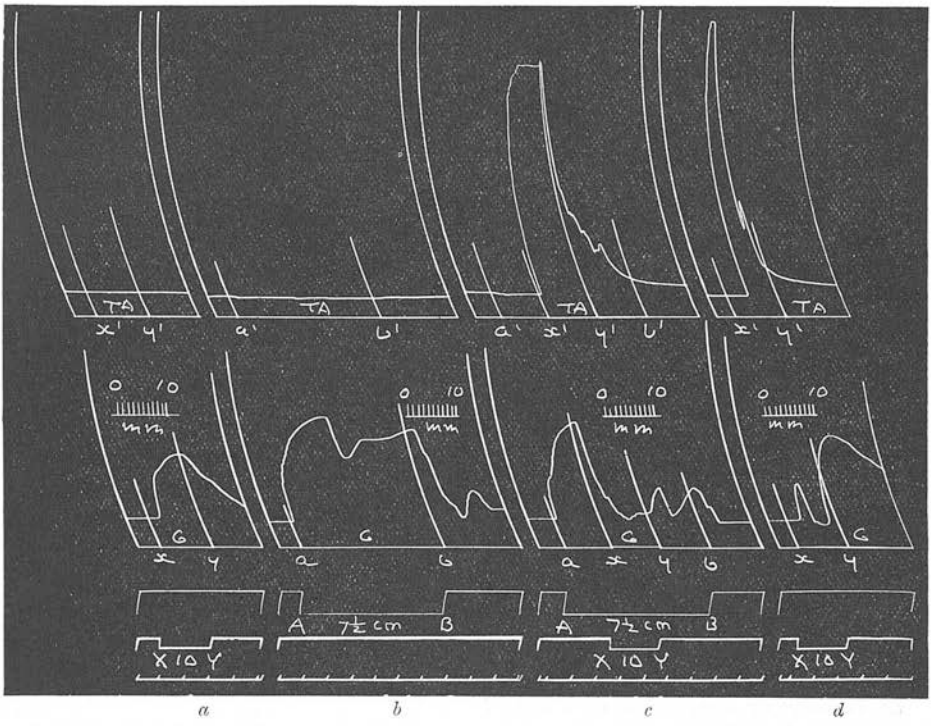


FIG. 20.—Experiment C, lxxvi., record 318, 8596 ; 13/5/13.—Decerebrate cat. Four reactions taken at minute intervals, 3 hours and 38 minutes after decerebration.

Reaction *a* is a "pure" ipsilateral extension-reflex, and reaction *b* is a "pure" contralateral extension-reflex. In *b* note that during stimulation there is a partial relaxation followed by a restitution of the maintained extensor contraction.

Reaction *c* is a compound one in which the contralateral stimulus gives the "background" of extension, and in which the stimuli compounded are of the same strengths as these used in *a* and *b*. Here during the period of double stimulation (ordinates $x$, $x'$–$y$, $y'$) there is a relaxation of maintained extension and a reciprocal flexor contraction. Note that in the third phase of the reaction (ordinates $y$, $y'$–$b$, $b'$) there is a continuation of the extensor depression of the period of double stimulation, although there is a partial extensor reconstitution of contraction.

In reaction *d* the "pure" ipsilateral stimulus is repeated. Here there is a primary extensor contraction in the period of stimulation, but this is followed by a reversal of the reaction to one of flexion while the stimulus is still running.

This compound reaction therefore demonstrates a reversal of the effect of the ipsilateral stimulus from one of abnormal direct extension to the usual flexion reaction.

The contralateral stimulus was kept of constant value, and the strength of the ipsilateral stimulus—starting from a strength which gave the flexion-reflex complicated with a late extensor contraction during stimulation—was decreased in succeeding reactions. The contralateral ("background") stimulus was commenced four seconds before the ipsilateral.

When the ipsilateral stimulus was comparatively strong a flexor contraction which was greater than that of the "pure" flexion-reflex was obtained during double stimulation, and it was accompanied by an extensor relaxation. As the duration of double stimulation continued this relaxation decreased in value—the decrement corresponding to the late extensor contraction in the "pure" flexion-reflex. With decrease of the strength of ipsilateral stimulation a point was reached at which the "pure" ipsilateral stimulus gave a reaction of extensor contraction unaccompanied by flexor contraction, but before the commencement of the extensor contraction there was a slight extensor relaxation—the reaction thus being of "decerebrate" type. When this was compounded with the contralateral stimulus there was a marked relaxation of the extensor contraction, accompanied by a very slight flexor contraction. As before, the extensor relaxation decreased during the period of double stimulation. A weaker ipsilateral stimulus gave an extensor contraction of "spinal" type. When this was compounded with the contralateral extension there was an extensor relaxation smaller than before, and no flexor contraction. Yet weaker ipsilateral stimulation gave no extensor contraction (or perhaps a very small contraction). When compounded with the contralateral extension there was a very slight extensor relaxation. Later in this same experiment a weak ipsilateral stimulus again evoked a reaction of extensor contraction of "spinal" type. When compounded with a contralateral extension-reflex there was again a slight extensor relaxation. When the ipsilateral stimulus was strong there was again an augmentation of the flexor contraction on the compounding of the two stimuli. This experiment was the same one as that in which the contralateral stimulus, when given after the commencement of the ipsilateral, evoked an augmentation of the flexor contraction, although when "pure" it gave extensor contraction alone.

In another experiment of this nature somewhat similar results were seen. When both the stimuli were evocative of extension it was found that the ipsilateral stimulus, if applied after the commencement of the contralateral, produced a slight relaxation of the contralateral extension. When the contralateral was applied after the commencement of the ipsilateral there was little or no change in the curve during the period of double stimulation. With greater strengths of ipsilateral stimulation extensor relaxation seemed to be conditioned by either stimulus when applied during the period of application of the other. With still greater strengths an augmentation of the flexor contraction was conditioned by the application of either stimulus during the application of the other. When the ipsilateral stimulus was applied during the period of application of the other the flexor contraction then first appeared, but was greater than in the "pure" ipsilateral reaction.

In yet other experiments similar phenomena have been observed.

In one of these (figs. 21, 22) it was found that, when a "background"

of contralateral extension was used, during double stimulation there was a slight augmentation of extension when the ipsilateral stimulus was very weak (and even when it was subliminal). At this strength the " pure " ipsilateral stimulus gave a very slight extensor contraction during stimulation.

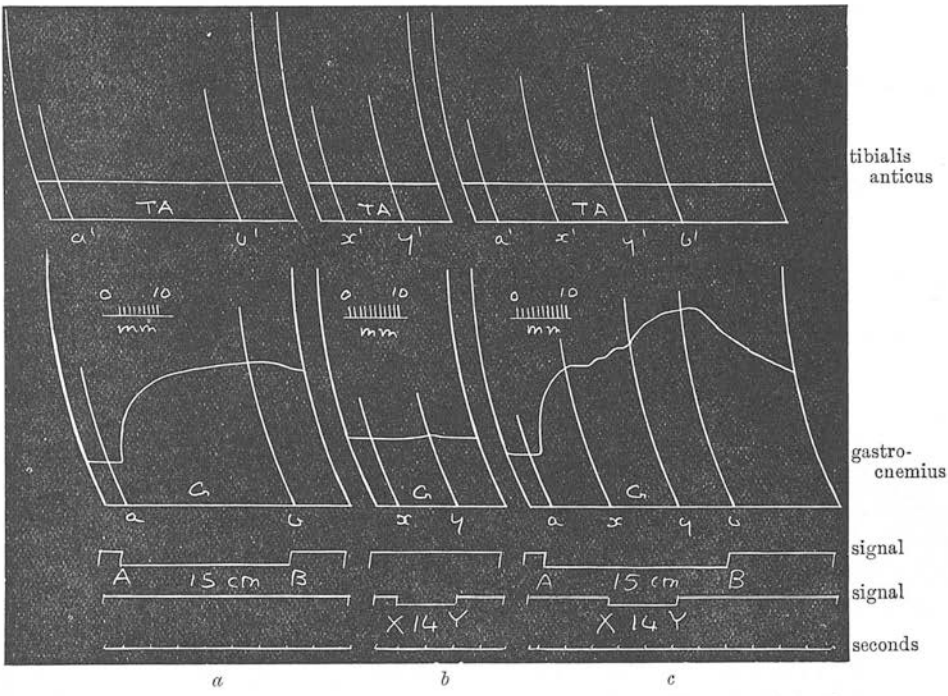


FIG. 21.—Experiment C, clv., record 278, 6622; 30/1/13.—Decerebrate cat. Three reactions, taken at minute intervals, obtained 3 hours and 10 minutes after decerebration.

Reaction *a* is a "pure" contralateral extension-reflex, for comparison with *c*—where the contralateral ("background") stimulus is of the same strength.

Reaction *b* is a "pure" ipsilateral one. There is a very slight extensor contraction of threshold value.

In the compound reaction *c* it will be observed that during double stimulation there is an augmentation of extensor contraction. The augmentation (estimated from the level of contraction which obtains in the "pure" contralateral reaction) is greater than the extensor contraction in *b*. The level attained is higher than any part of the "pure" contralateral reflex (*a*). There is therefore here a summation of the abnormal ipsilateral extension-reflex and of the normal contralateral extension-reflex—and this summation is greater than a simple algebraic summation of the two.

Observe that in the "third phase" of the compound reaction—that is, the phase after withdrawal of the ipsilateral stimulus and when the contralateral "background" is still in action (between ordinates *y*, *y'* and *b*, *b'*)—there is a further augmentation of extensor contraction. This is, as it were, a rebound effect from the ipsilateral stimulus; but there is no corresponding rebound in the "pure" ipsilateral reflex (*b*).

With stronger ipsilateral stimuli (the strength of contralateral stimulation remaining constant) there was, during the period of double stimulation, first a slight extensor relaxation and then an augmentation of extensor contraction. With yet stronger ipsilateral stimuli there was relaxation of extensor contraction alone during double stimulation—even at a strength

of ipsilateral stimulation which when applied "pure" gave extensor contraction.

After this series was terminated another series, in which the two stimuli were commenced and terminated synchronously, was taken. The contralateral stimulus was again of constant strength, and the value of the ipsilateral stimulus was progressively increased in succeeding reactions (fig. 23). Here with weak ipsilateral stimuli there was in the compound reaction an extensor contraction which was of greater extent than the extensor contraction of the "pure" contralateral extension-reflex. With progressive increase in the strengths of the ipsilateral stimuli the extents of extensor contraction during double stimulation decreased. With strong ipsilateral stimuli the extent was no more than in the "pure" contralateral extension-reflex; with still stronger ipsilateral stimuli the extent was smaller; and with the strongest ipsilateral stimuli used there was, during double stimulation, extensor relaxation and flexor contraction. At the end of the series a compound reaction in which the ipsilateral stimulus was again weak demonstrated an extensor contraction again greater than in the "pure" contralateral extension-reflex.

Later in this experiment a similar series was taken. The contralateral stimulus used was stronger than before. Here the augmentation of extension with weak ipsilateral stimuli was not seen; but the relative depression of extension during double stimulation was marked—even at strengths of ipsilateral stimulation which, when applied "pure," gave an ipsilateral extension-reflex.

Yet later in the same experiment the movements of the soleus portion alone of gastrocnemius-soleus were registered (of course in conjunction with the reciprocal movements of tibialis anticus). Here it was found that the phenomenon of extensor contraction during weak ipsilateral stimuli was evidenced in soleus; a point of importance, because soleus is a pure extensor of the ankle joint, whereas gastrocnemius is a double joint muscle and might act as a knee flexor (simultaneous records of soleus and gastrocnemius, however, demonstrate that the gastrocnemius portion of the muscle acts in every way like the soleus portion —that is, that it acts as a pure extensor of the ankle). The same phenomena of extensor augmentation when the ipsilateral stimulus was weak, and of relative extensor depression when the ipsilateral stimulus was stronger (even when at that strength in a "pure" reaction it evoked extension), were observed.

In another experiment somewhat similar results were obtained. Here in the first place was obtained a series of compound reactions in which the contralateral stimulus was kept of constant value, but in which the value of the ipsilateral stimulus was progressively increased. At each value of ipsilateral stimulation the two stimuli were compounded, firstly, with the ipsilateral as the "background," and secondly, with the "background" the contralateral stimulus.

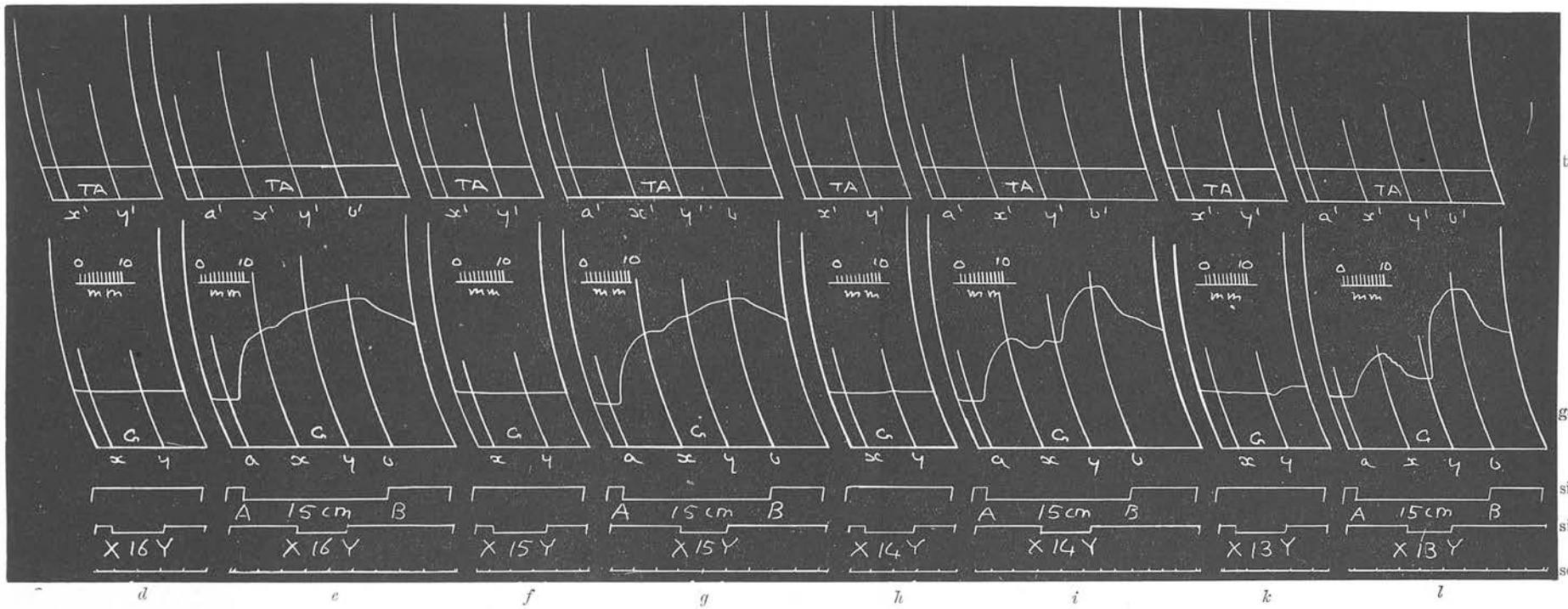


FIG. 22.—Experiment C, clv., record 278, 6625 ; 30/1/13.—Decerebrate cat. Eight reactions, taken at minute intervals, obtained 3 hours and 13 minutes after decerebration. The first reaction here follows the last reaction in fig. 21, at an interval of 1 minute. The contralateral "background" stimulus remains of the same strength throughout—that is, the same as reaction *a* of fig. 21. Note, however, that its value falls—as is seen by the fact that the first phase (between ordinates *a*, *a'* and *x*, *x'*) exhibits a less degree of extensor contraction towards the end of the series.

Reactions *d*, *f*, *h*, and *k* are "pure" ipsilateral reactions of the same strength of stimulus as that used in the compound reactions which respectively succeed them. Reactions *d* and *f* (strength weaker than in the preceding figure) are subliminal. Reaction *h* is one of slight ipsilateral extension. In *k* there is extensor relaxation but no flexor contraction. With stronger "pure" ipsilateral stimuli flexor contraction during stimulation appeared. Note in *k* the presence of a slight "extensor rebound relaxation after inhibition" followed by a later extensor rebound contraction.

Reactions *e*, *g*, *i*, and *l* are compound with a contralateral "background." In the first two there is extensor augmentation during double stimulation—although in the second (*g*) there is perhaps a very slight retardation of extensor contraction in the first part of the period of double stimulation. In the third (*i*) there is distinct extensor relaxation during double stimulation, followed later in the period of double stimulation by partial restitution. In the fourth (*l*) there is nothing but extensor relaxation. Note in the third and fourth compound reactions (*i* and *l*) the hint at a rhythmic phenomenon during double stimulation.

In the third phases of the compound reactions augmentation (or restitution) of extensor contraction occurs. This is to a height greater than that at the corresponding point in the "pure" extension-reflex (see fig. 21). In level of height attained this is greater the stronger the ipsilateral stimulus is. In *l* note the slight flattening (it is hardly a "notch") in the curve of extensor restitution in the third phase. This seems to be related to the "extensor rebound relaxation after inhibition" evident in the corresponding "pure" ipsilateral reaction (*k*).

In the fourth phases there is extensor after-discharge, which appears to be less well sustained the stronger the ipsilateral stimulus is.

This series therefore demonstrates that increase of the strength of a nearly threshold value of ipsilateral stimulation may change the reaction during double stimulation in a compound reaction from extensor augmentation to extensor depression, even although the "pure" ipsilateral stimulus which gives that depression may itself give extensor contraction during stimulation (*h*).

Note here that there is a further extensor augmentation in the third phase of the compound reactions—between ordinates *y*, *y'* and *b*, *b'*. This successive effect of extensor augmentation after double stimulation increases absolutely with increase in the strength of the ipsilateral stimulus.

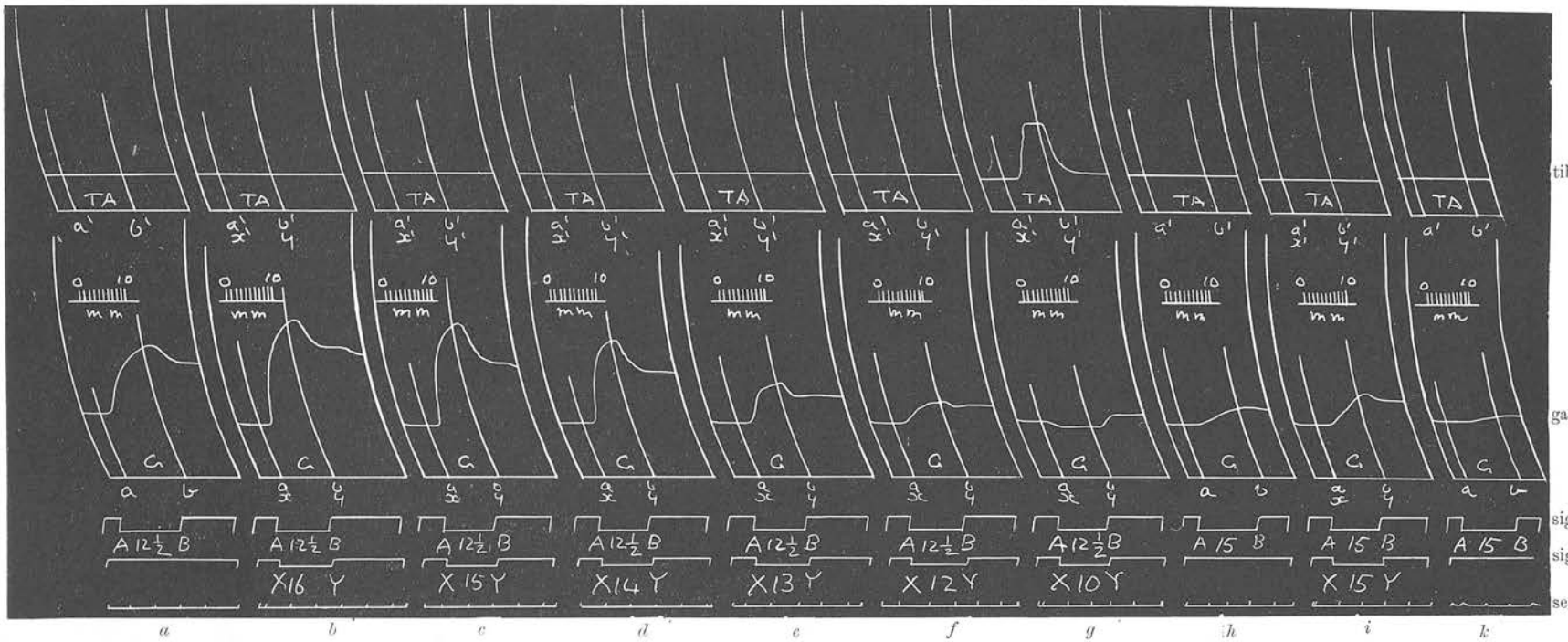


FIG. 23.—Experiment C, clv., record 278, 6638 ; 30/1/13.—Decerebrate cat. A series of ten reactions—taken at minute intervals—obtained 3 hours and 26 minutes after decerebration. From the same experiment as the two preceding figures.

Reaction *a* is a "pure" contralateral one taken at a strength of stimulus which is used unchanged throughout the series except in the three final reactions. Reactions *h* and *k* are also "pure," but taken with a weaker stimulus. Reaction *h* is of the same extent as a similar one taken immediately before the series, and it may be inferred that the value of the stronger contralateral stimulus used in *a*–*g* remained for all practical purposes constant.

The other reactions are compound. The two stimuli are simultaneously commenced and terminated, and the strength of the ipsilateral stimulus is progressively increased throughout the series.

In *b* there is an augmentation of extensor contraction during double stimulation to an extent greater than in the "pure" contralateral extension-reflex. As the strength of ipsilateral stimulation is increased this augmentation drops in value until, in *e*, it is a depression of extensor contraction as compared with the "pure" contralateral extension-reflex. Finally, in *g*, there is no extensor contraction, but actually extensor relaxation during double stimulation, and a reciprocal flexor contraction. Reaction *i* is a repetition of *c*, but with a weaker contralateral stimulus, and there is again clearly extensor augmentation, although much smaller than in *c*.

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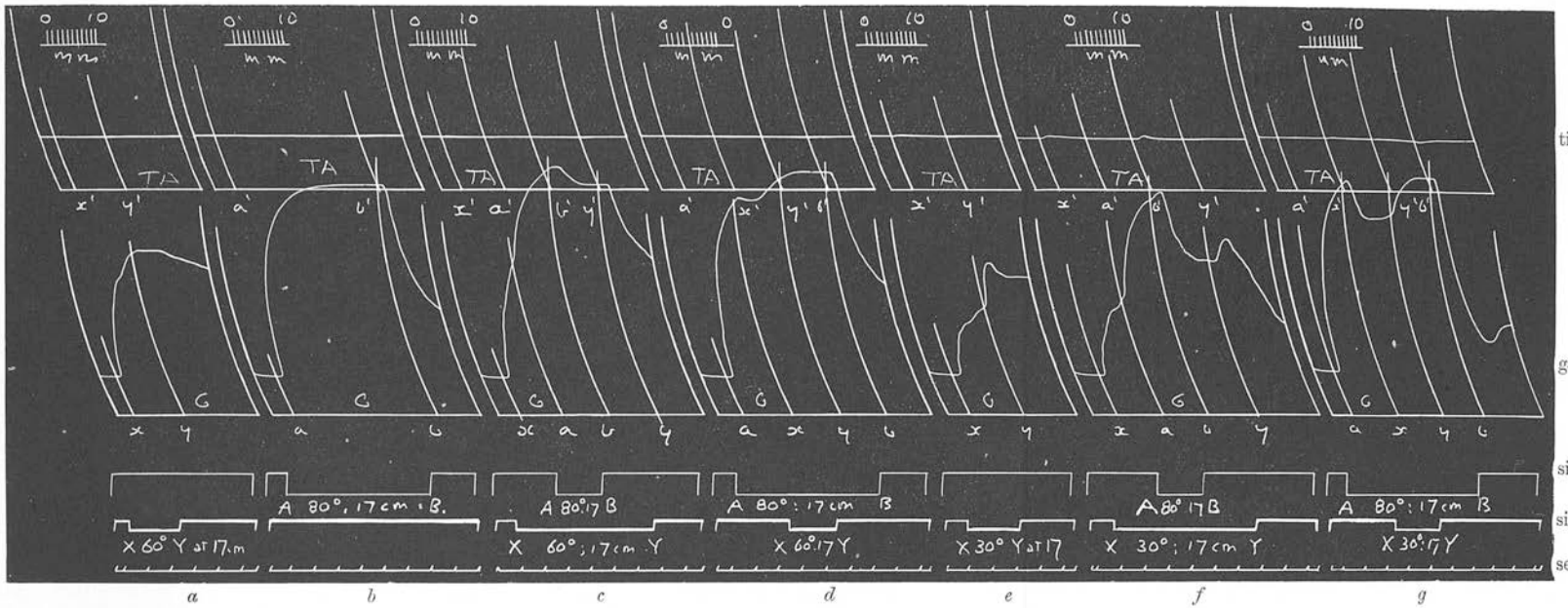


FIG. 24.—Experiment C, clxix., record 300, 7745 ; 28/2/13.—Decerebrate cat. A series of seven reactions—taken at minute intervals—obtained 2 hours and 48 minutes after decerebration. Throughout the series the strength of contralateral stimulation remains constant. The ipsilateral stimulus is varied.

Reaction *a* is a "pure" ipsilateral extension-reflex, and reaction *b* is a "pure" contralateral extension-reflex of the strength used throughout the series.

Reaction *c* is compounded of *a* and *b*—the "background" being the ipsilateral stimulus. Note that in the period of double stimulation there is an augmentation of extensor contraction to a greater level than that which obtains in the "pure" contralateral reaction. Note also that in the third phase of the reaction the level of extensor contraction remains augmented.

Reaction *d* is a compound one with the contralateral stimulus as "background." Here there is extensor relaxation during double stimulation. This, however, during the period of double stimulation, passes over to contraction and augmentation ; and the augmentation of extensor contraction (as compared with the "pure" contralateral reaction) persists as a successive effect of double stimulation. Compare the extent of extensor contraction during double stimulation in *c* and *d* and note that it is higher in *c* than in *d*.

Reaction *e* is a "pure" ipsilateral extension-reflex obtained with a stronger stimulus than that used in *a*.

Reactions *f* and *g* are similar to *c* and *d* but taken with the stronger ipsilateral stimulus. Note here that the extent of extensor contraction during double stimulation is still greater in *f* than in *g*, but that when *f* is compared with *c* the level of extensor contraction during double stimulation is less ; as it also is less in *g* than in *d*. Note, in *f*, that here the level of extensor contraction during double stimulation is lower than in the "pure" contralateral reaction.

Note here, in comparing *f* with *c*, that in *f* there is a greater extensor relaxation on cessation of the period of double stimulation than in *c*, and that on cessation of the ipsilateral "background" stimulus in *f* there is an extensor rebound contraction—not present in *c* but present in *e*. On comparing *g* with *d* note that the extensor relaxation during double stimulation is more lasting in *g*, and that the subsequent augmentation of extensor contraction in the third phase of the compound reaction is not so great.

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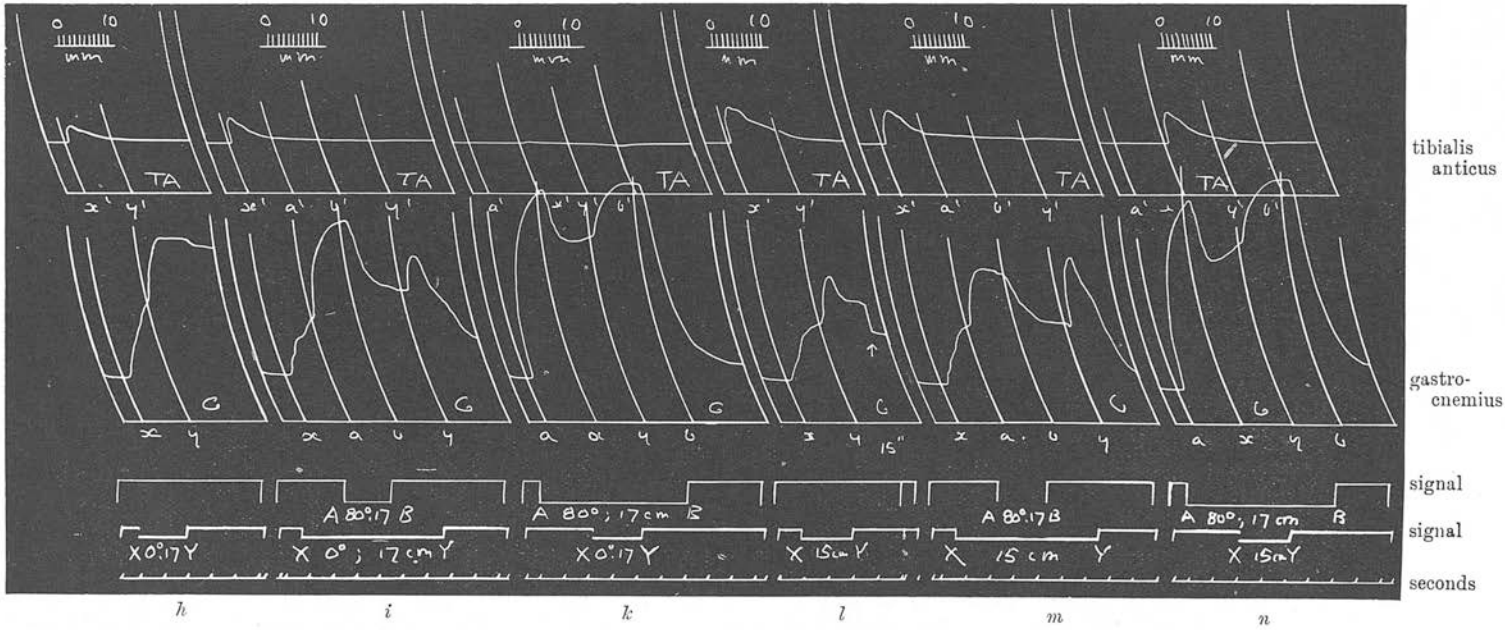


FIG 25.—Experiment C, clxix., record 300, 7752 ; 28/2/13.—Decerebrate cat. A series of six reactions—taken at minute intervals—obtained 2 hours and 55 minutes after decerebration. This figure is a direct continuation of fig. 24—one minute elapses between the last reaction in that figure and the first in this.

Reaction *h* is a "pure" ipsilateral one taken with a yet stronger stimulus. Note the greater maintenance of the extensor rebound contraction in *h* than in *l*.

Reactions *i* and *k* are compound ones similar to those in the previous figure. In *i* the extensor augmentation during double stimulation is less than before, and the subsequent relaxation is greater. In *k* the extensor relaxation during double stimulation is greater than before, and the subsequent augmentation is about the same. Note that the level of extensor contraction during double stimulation is still higher in *i* (ipsilateral "background") than in *k* (contralateral "background"). Note in *i* and *m* the terminal phenomena.

Reactions *l*, *m*, and *n* are similar to *h*, *i*, *k*, but with a stronger ipsilateral stimulus. Note here a still less extent of extensor contraction during double stimulation in *m* than in *i*, and a greater subsequent depression. Also note in *n* a still greater extensor depression during double stimulation than in *k*—but a similar subsequent augmentation. On comparing *m* with *n* it will be seen that the level of extensor contraction during double stimulation is greater in *n* than in *m*.

This whole series (figs. 23, 24) demonstrates well the effect upon the summation of the two reactions of changing strength of stimulus, and the differences conditioned by "background." Refer also to xvi. fig. 16, which is a direct continuation of this figure and completes the series.

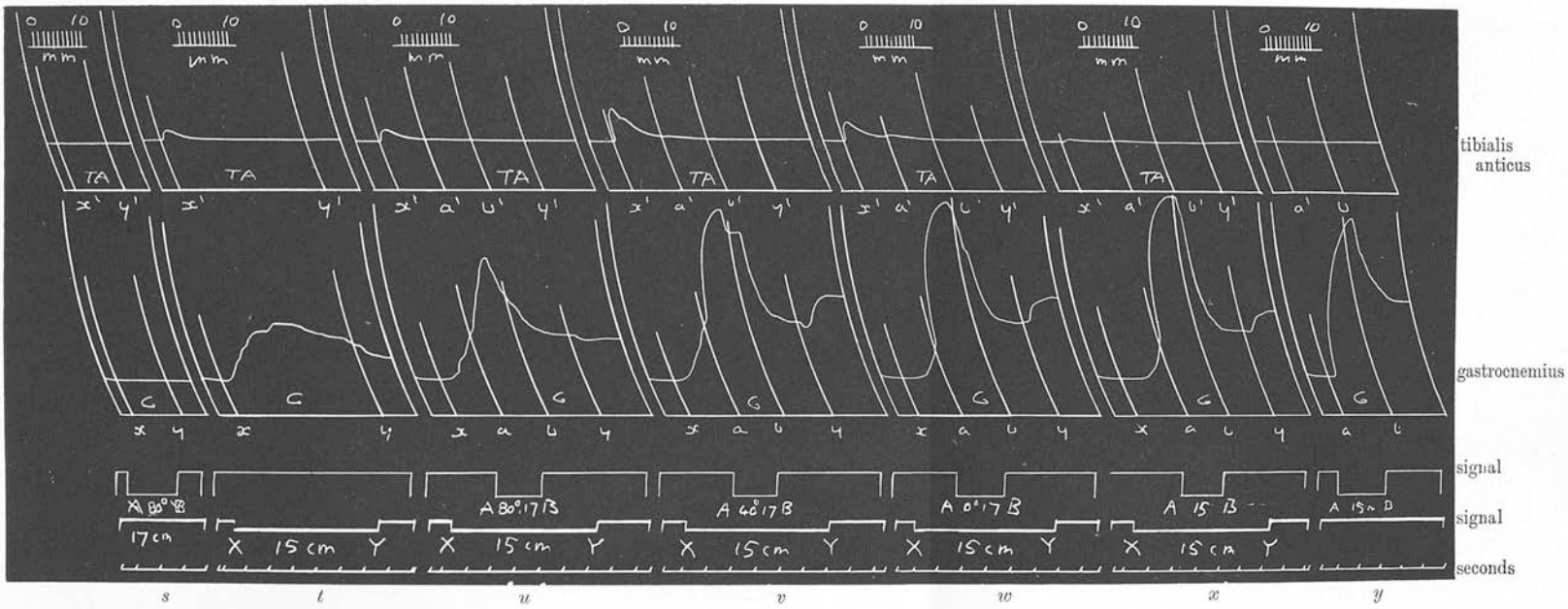


FIG. 26.—Experiment C, clxix., record 300, 7781 ; 38/2/13.—Decerebrate cat. A series of seven reactions taken at minute intervals and 3 hours and 25 minutes after decerebration. This figure is a direct continuation of the series in xvi. figs. 17, 18, and 19, and reaction *s* here follows reaction *r* of xvi. fig. 19, at an interval of 1 minute.

Reaction *s* is a "pure" subliminal contralateral reflex taken with the strength of contralateral stimulation used in reaction *u*.

Reaction *t* is a "pure" ipsilateral reflex taken with the same duration and strength of stimulation used in the following reactions in this series.

Reaction *u* is compounded of *s* and *t*. Here the contralateral stimulus (which when applied "pure" is subliminal) during double stimulation conditions an increase in extensor contraction. Here therefore there is summation of the extension effects of the two stimuli. [The same sort of summation was seen in a previous reaction in which the strengths of the two stimuli were the same as in this one, but in which the subliminal contralateral stimulus served as the "background."]

Reactions *v*, *w*, and *x* are similar compound ones in which the strength of the interrupting contralateral stimulus is progressively increased. Note the increase in the level of extensor contraction during double stimulation with increase in the strength of the contralateral stimulus. Note the level of extensor contraction which persists after withdrawal of the contralateral stimulus—this seems to fall. And note the extensor rebound on withdrawal of the ipsilateral stimulus. This is not present in the "pure" ipsilateral reaction (*t*) nor in a "pure" contralateral reaction taken at the strength of stimulus used in *x* (*y*).

Reaction *y* is a final "pure" contralateral extension-reflex obtained with the strength of stimulus used in *x*. Note that it is of smaller extent of extensor contraction than that which obtains during double stimulation in *x*—so that there is, therefore, augmentation of extensor contraction during double stimulation in that reaction. There the rapidity of increasing extensor contraction is also greater. Note also that in this "pure" reaction there is an extensor after-discharge —but no rebound contraction. In *x* the level of extensor contraction in the third phase of the compound reaction (that is, between ordinates *b*, *b'* and *y*, *y'*) is lower than is the level of this after-discharge.

This figure therefore illustrates a summation of ipsilateral and contralateral extension at all the strengths of contralateral stimulation used.

In this series it was found that at every strength of ipsilateral stimulation used there was increase of extensor contraction during double stimulation when the "background" stimulus was the ipsilateral, and decrease of extensor contraction when the "background" stimulus was the contralateral. Throughout the series it was found that as the strength of ipsilateral stimulation was increased there was a lesser increase of extension during double stimulation against the ipsilateral "background" and a greater relaxation of extensor contraction against the contralateral "background" (figs. 24, 25, and xvi. fig. 16).

In this series it was interesting to compare the levels of extensor contraction during double stimulation against the two "backgrounds." With very weak ipsilateral stimuli, during double stimulation against the ipsilateral "background" there was augmentation of extensor contraction to a level greater than that which obtained in the "pure" contralateral extension-reflex. That is to say, that there was summation of the two extension effects. [The time relations of the stimuli used were such that the "background" stimulus was started about two seconds before the application of the interrupting stimulus; double stimulation lasted for two seconds; and the "background" stimulus was then allowed to continue alone for another two seconds.] On the other hand, against the contralateral "background" there was a slight extensor relaxation during double stimulation. Thus with weak ipsilateral stimuli there was a greater level of extensor contraction during double stimulation against the ipsilateral "background" than against the contralateral. As the strength of ipsilateral stimulation was increased the level of extensor contraction during double stimulation—against either "background"—fell. But it did not fall equally in these two cases. It fell more rapidly in the case of double stimulation against an ipsilateral "background." Thus there was a certain strength of ipsilateral stimulation at which the levels of extensor contraction during double stimulation in the two cases were very nearly equal; and with increased strengths of ipsilateral stimulation it was found that the level of extensor contraction during double stimulation against the ipsilateral "background" was smaller than that against the contralateral "background."

Shortly after this series was obtained other series was recorded (xvi. figs. 17, 18, 19, and fig. 26 of this paper).

In the first place, a set of three series with a contralateral "background" stimulus were registered. In each of these the ipsilateral interrupting stimulus was of constant value (of different strengths in the three series), but the contralateral "background" was progressively increased in strength. With a weak ipsilateral interrupting stimulus and a subliminal contralateral "background" it was found that during double stimulation there was augmentation of extensor contraction to a level higher than that in the "pure" ipsilateral extension-reflex. But with supraliminal contralateral "backgrounds" there was extensor relaxation during double stimulation. This relaxation was of course down from the level of extensor contraction

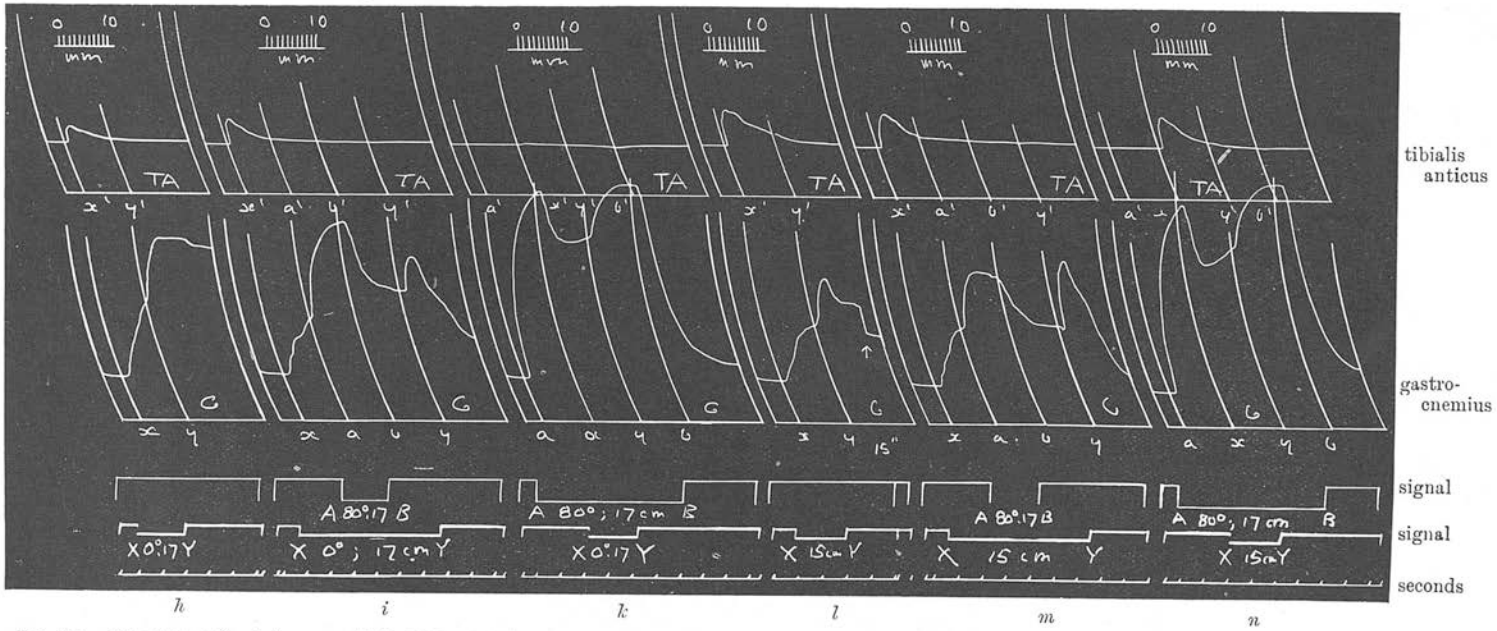


FIG 25.—Experiment C, clxix., record 300, 7752; 28/2/13.—Decerebrate cat. A series of six reactions—taken at minute intervals—obtained 2 hours and 55 minutes after decerebration. This figure is a direct continuation of fig. 24—one minute elapses between the last reaction in that figure and the first in this.

Reaction *h* is a "pure" ipsilateral one taken with a yet stronger stimulus. Note the greater maintenance of the extensor rebound contraction in *h* than in *l*.

Reactions *i* and *k* are compound ones similar to those in the previous figure. In *i* the extensor augmentation during double stimulation is less than before, and the subsequent relaxation is greater. In *k* the extensor relaxation during double stimulation is greater than before, and the subsequent augmentation is about the same. Note that the level of extensor contraction during double stimulation is still higher in *i* (ipsilateral "background") than in *k* (contralateral "background"). Note in *i* and *m* the terminal phenomena.

Reactions *l*, *m*, and *n* are similar to *h*, *i*, *k*, but with a stronger ipsilateral stimulus. Note here a still less extent of extensor contraction during double stimulation in *m* than in *i*, and a greater subsequent depression. Also note in *n* a still greater extensor depression during double stimulation than in *k*—but a similar subsequent augmentation. On comparing *m* with *n* it will be seen that the level of extensor contraction during double stimulation is greater in *n* than in *m*.

This whole series (figs. 23, 24) demonstrates well the effect upon the summation of the two reactions of changing strength of stimulus, and the differences conditioned by "background." Refer also to xvi. fig. 16, which is a direct continuation of this figure and completes the series.

In this series it was found that at every strength of ipsilateral stimulation used there was increase of extensor contraction during double stimulation when the "background" stimulus was the ipsilateral, and decrease of extensor contraction when the "background" stimulus was the contralateral. Throughout the series it was found that as the strength of ipsilateral stimulation was increased there was a lesser increase of extension during double stimulation against the ipsilateral "background" and a greater relaxation of extensor contraction against the contralateral "background" (figs. 24, 25, and xvi. fig. 16).

In this series it was interesting to compare the levels of extensor contraction during double stimulation against the two "backgrounds." With very weak ipsilateral stimuli, during double stimulation against the ipsilateral "background" there was augmentation of extensor contraction to a level greater than that which obtained in the "pure" contralateral extension-reflex. That is to say, that there was summation of the two extension effects. [The time relations of the stimuli used were such that the "background" stimulus was started about two seconds before the application of the interrupting stimulus; double stimulation lasted for two seconds; and the "background" stimulus was then allowed to continue alone for another two seconds.] On the other hand, against the contralateral "background" there was a slight extensor relaxation during double stimulation. Thus with weak ipsilateral stimuli there was a greater level of extensor contraction during double stimulation against the ipsilateral "background" than against the contralateral. As the strength of ipsilateral stimulation was increased the level of extensor contraction during double stimulation—against either "background"—fell. But it did not fall equally in these two cases. It fell more rapidly in the case of double stimulation against an ipsilateral "background." Thus there was a certain strength of ipsilateral stimulation at which the levels of extensor contraction during double stimulation in the two cases were very nearly equal; and with increased strengths of ipsilateral stimulation it was found that the level of extensor contraction during double stimulation against the ipsilateral "background" was smaller than that against the contralateral "background."

Shortly after this series was obtained other series was recorded (xvi. figs. 17, 18, 19, and fig. 26 of this paper).

In the first place, a set of three series with a contralateral "background" stimulus were registered. In each of these the ipsilateral interrupting stimulus was of constant value (of different strengths in the three series), but the contralateral "background" was progressively increased in strength. With a weak ipsilateral interrupting stimulus and a subliminal contralateral "background" it was found that during double stimulation there was augmentation of extensor contraction to a level higher than that in the "pure" ipsilateral extension-reflex. But with supraliminal contralateral "backgrounds" there was extensor relaxation during double stimulation. This relaxation was of course down from the level of extensor contraction

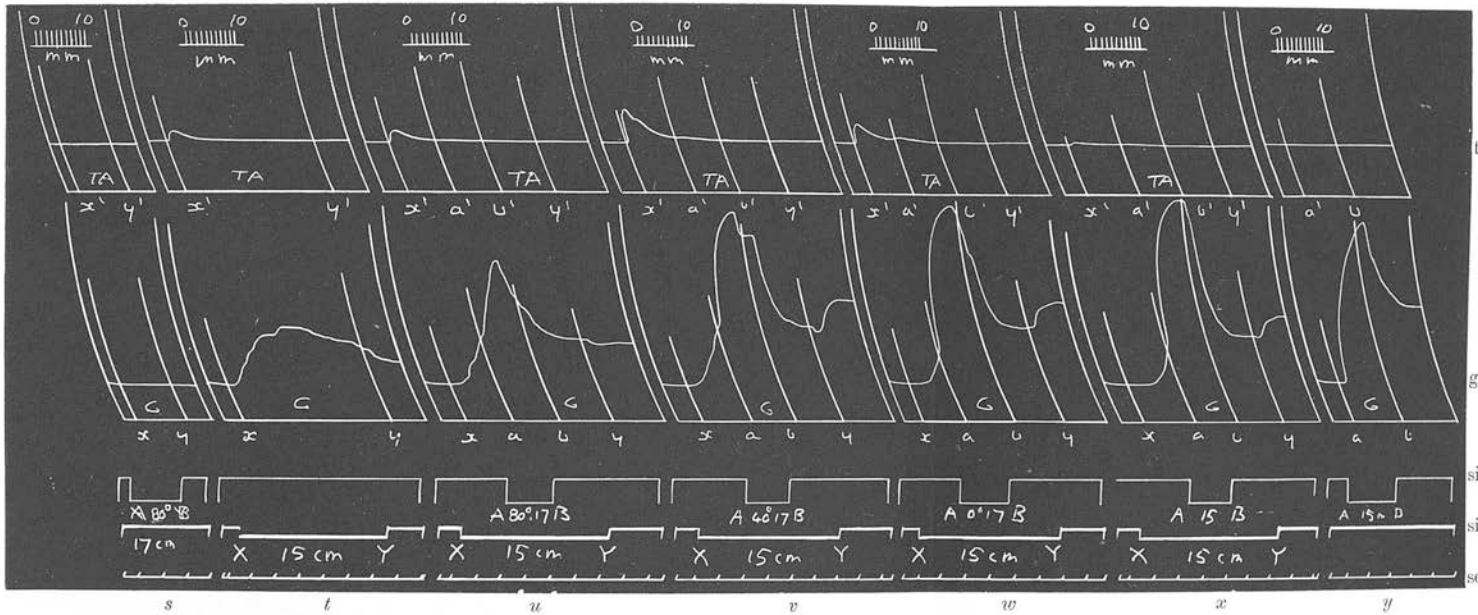


FIG. 26.—Experiment C, clxix., record 300, 7781; 38/2/13.—Decerebrate cat. A series of seven reactions taken at minute intervals and 3 hours and 25 minutes after decerebration. This figure is a direct continuation of the series in xvi. figs. 17, 18, and 19, and reaction *s* here follows reaction *r* of xvi. fig. 19, at an interval of 1 minute.

Reaction *s* is a "pure" subliminal contralateral reflex taken with the strength of contralateral stimulation used in reaction *u*.

Reaction *t* is a "pure" ipsilateral reflex taken with the same duration and strength of stimulation used in the following reactions in this series.

Reaction *u* is compounded of *s* and *t*. Here the contralateral stimulus (which when applied "pure" is subliminal) during double stimulation conditions an increase in extensor contraction. Here therefore there is summation of the extension effects of the two stimuli. [The same sort of summation was seen in a previous reaction in which the strengths of the two stimuli were the same as in this one, but in which the subliminal contralateral stimulus served as the "background."]

Reactions *v*, *w*, and *x* are similar compound ones in which the strength of the interrupting contralateral stimulus is progressively increased. Note the increase in the level of extensor contraction during double stimulation with increase in the strength of the contralateral stimulus. Note the level of extensor contraction which persists after withdrawal of the contralateral stimulus—this seems to fall. And note the extensor rebound on withdrawal of the ipsilateral stimulus. This is not present in the "pure" ipsilateral reaction (*t*) nor in a "pure" contralateral reaction taken at the strength of stimulus used in *x* (*y*).

Reaction *y* is a final "pure" contralateral extension-reflex obtained with the strength of stimulus used in *x*. Note that it is of smaller extent of extensor contraction than that which obtains during double stimulation in *x*—so that there is, therefore, augmentation of extensor contraction during double stimulation in that reaction. There the rapidity of increasing extensor contraction is also greater. Note also that in this "pure" reaction there is an extensor after-discharge—but no rebound contraction. In *x* the level of extensor contraction in the third phase of the compound reaction (that is, between ordinates *b*, *b'* and *y*, *y'*) is lower than is the level of this after-discharge.

This figure therefore illustrates a summation of ipsilateral and contralateral extension at all the strengths of contralateral stimulation used.

in the contralateral reaction, but it did not bring that level down to the level of extensor contraction in the "pure" ipsilateral extension-reflex. The stronger the contralateral "background" was the smaller was the extent of this extensor relaxation—that is, the greater was the level of extensor contraction during double stimulation. The same phenomena were observed with the other strengths of interrupting ipsilateral stimuli. It is curious that with the strongest ipsilateral stimulus used in these series, although the extensor relaxation during double stimulation decreased with increase in the strength of the contralateral "background," yet the flexor contraction during double stimulation (for at that strength there was an ipsilateral flexion-reflex) also increased.

In a final set of series the ipsilateral stimulus was used as the "background" (being varied in strength within each series), while the contralateral stimulus was used as the interrupting stimulus (being constant within a series but varied in strength in the different series). Here in every case the value of extensor contraction during double stimulation was greater than in the corresponding "pure" contralateral extension-reflex, and that value rose with increase in the strength of the interrupting contralateral stimulus. When a subliminal contralateral stimulus was used there was yet a distinct augmentation of extensor contraction during double stimulation. On comparing the separate series together it was seen that the extensor contraction during double stimulation was smaller the stronger was the "background" ipsilateral stimulus.

### B. Ipsilateral Flexion and Contralateral Flexion.

1. Contralateral Stimulus commenced before the Commencement of the Ipsilateral.—In these experiments the ipsilateral flexion-producing stimulus has been applied during the application of the contralateral stimulus, which also gave a reaction of flexion. The result of this is to give an augmentation of the flexor contraction conditioned by the contralateral stimulus. But in the experiments examined the extent of the flexor contraction during double stimulation has sometimes been smaller than that of the flexor contraction in the "pure" ipsilateral flexion-reflex evoked at the same strength of stimulus as that used in the compounded reaction. In one experiment the contralateral reaction was one of abnormal primary flexion, sometimes followed by late extensor contraction and flexor relaxation. The ipsilateral stimulus also evoked a reaction of "decerebrate" type, but the element of extensor contraction was small. When the contralateral stimulus was applied there was no element of extensor contraction in the period of four seconds in which it ran alone. When the ipsilateral stimulus was then applied there was an immediate augmentation of the flexor contraction—but not to the extent of contraction attained in the "pure" ipsilateral flexion-reflex. The flexor contraction then immediately began to fall again; and at the same time there appeared an

extremely well-marked extensor contraction, which gradually increased in extent throughout the remainder of the period of double stimulation.

In other experiments of this nature, although the ipsilateral stimulus again produced an augmentation of the abnormal contralateral flexor contraction in being at the time of its application, there was no extensor contraction produced. As before, the augmented flexor contraction during double stimulation was not of so great extent as that of the flexor contraction in the "pure" flexion-reflex evoked at the same strength of ipsilateral stimulation (fig. 27).

But sometimes there is augmentation of flexion during double stimulation, so that the level of flexor contraction attained is greater than in either of the "pure" flexion-reflexes compounded (fig. 28). In such experiments it may happen that the contralateral reaction, either later or earlier in the experiment, is one of normal extension; and even then it often happens that this augmentation of flexion—above the level which obtains in the "pure" ipsilateral reflex—is seen during double stimulation in compound reactions. This phenomenon is seen occasionally in experiments in which no crossed flexion-reflex occurs, and it perhaps is conditioned by a state of the centres similar to that which conditions the abnormal crossed flexion-reflex.

2. Ipsilateral Stimulus commenced before the Commencement of the Contralateral.—The contralateral flexion reaction usually gives a smaller extent of flexor contraction than does the ipsilateral flexion. If the ipsilateral flexion is in being, two possibilities with regard to the flexor contraction during an added contralateral stimulation present themselves. For there may either be an augmentation of the flexor contraction or a depression of it.

No clear case of the second of these possibilities has presented itself, although approximations to it have been noticed

In one of these experiments there appeared to be a very slight reduction of the maintained flexor contraction of the ipsilateral stimulus when a contralateral stimulus was added to it, but the amount of relaxation was too small to admit of any certainty.

In another experiment the contralateral stimulus at one period gave a reaction characterised by a comparatively small flexor contraction followed by a later extensor contraction (7, fig. 34). When the contralateral stimulus was then applied during the application of the ipsilateral, there was at first a small augmentation of the flexor contraction; but this was soon followed by relaxation accompanied by extensor contraction which, however, was not so great as in the case when the ipsilateral stimulus was applied during the period of the contralateral.

In another similar experiment the contralateral stimulus evoked a similar reaction (7, fig. 36). Here again there was an immediate augmentation of the flexor contraction when the contralateral stimulus was applied during the period of the ipsilateral. This soon gave place to a

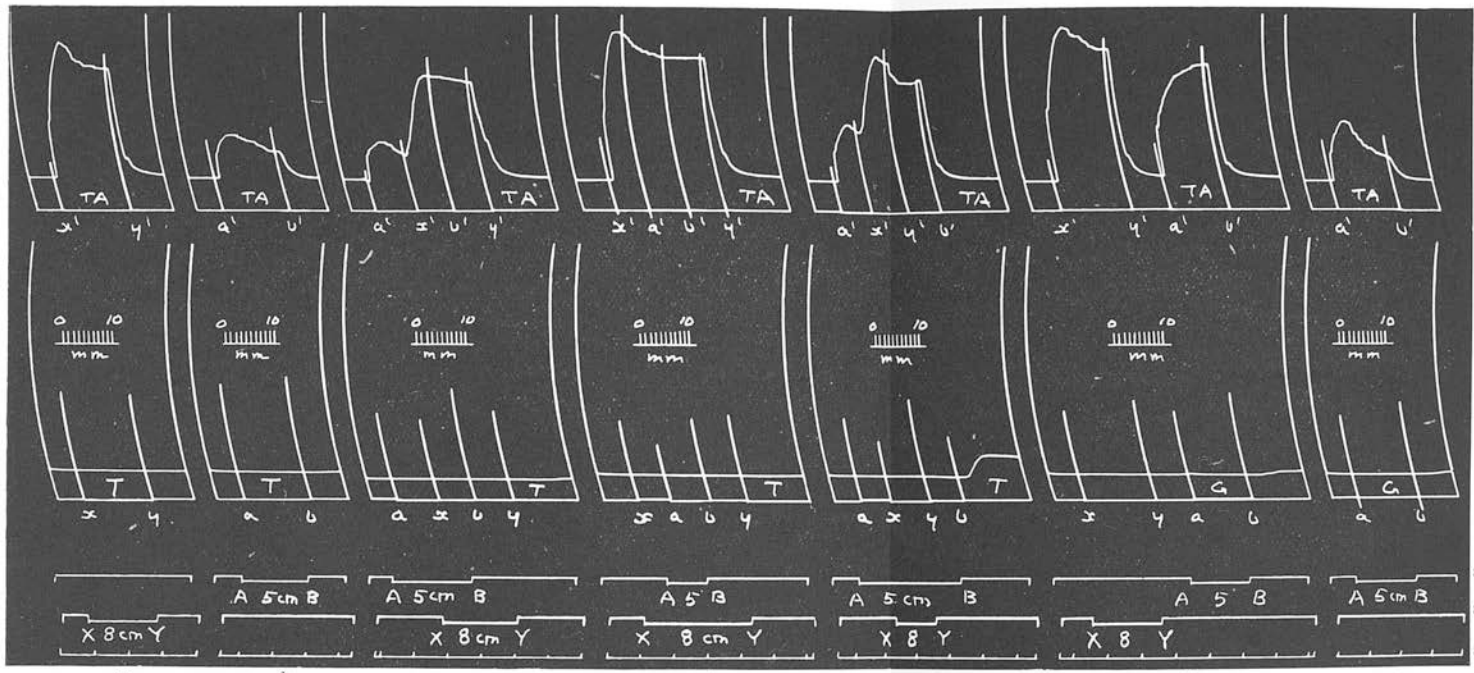


FIG. 27.—Experiment C, cxxxii., record 250, 5858 ; 14/11/12.—Decerebrate cat. A series of seven reactions taken at minute intervals 40 minutes after decerebration, and exhibiting an abnormal contralateral flexion-reflex compounded with a normal ipsilateral flexion-reflex.

Reaction *a* is a "pure" ipsilateral flexion-reflex taken with the same strength of ipsilateral stimulation which is used in the other reactions of the series. The first reaction in *f* is a similar "pure" ipsilateral flexion-reflex taken towards the end of the series. It is very similar to that in *a*.

Reaction *b* is a "pure" abnormal contralateral flexion-reflex taken with the same strength of contralateral stimulation used in the other reactions of the series. So is reaction *g*—note that it is very similar to reaction *b*.

Reaction *c* is a compound one in which the stimuli are in "step" arrangement. During double stimulation (ordinates *x*, *x'–b*, *b'*) there is an increase of the level of flexor contraction—but not up to the level which obtains in the "pure" ipsilateral reactions (*a* and *f*). On withdrawal of the contralateral stimulus the level of flexor contraction is maintained, there being no further increase.

Reaction *d* is a compound one of the usual arrangement of stimuli. Here the "background" is one of ipsilateral flexion, and there is little or no change in the curve during the period of double stimulation.

Reaction *e* is a compound one, again of the usual arrangement of stimuli but with a contralateral flexion "background." Note that during the period of double stimulation the level of flexor contraction attained is not so great as in the "pure" ipsilateral reflex. Note also that on withdrawal of the ipsilateral stimulus there is a sustentation of the level of flexor contraction, although at that point in a "pure" contralateral reaction the level of flexor contraction was very low. The effect of the contralateral stimulus is therefore augmented in this third phase of the reaction (ordinates *y*, *y'–b*, *b'*) Note here the marked extensor rebound contraction—of "tonic" type—on withdrawal of the contralateral "background" stimulus. This is not present in the other reactions of the series except, faintly, in *f*.

In reaction *f* an ipsilateral stimulus is first applied and withdrawn, and then, after an interval of about 1 second, a contralateral is applied for a similar length of time. Comparison of the contralateral reaction with the "pure" contralateral reactions (*b* and *g*) demonstrates that here there is a marked successive augmentation, conditioned by the previous ipsilateral reflex, of the contralateral reaction. Note the faint extensor rebound contraction on withdrawal of the contralateral stimulus. In this connexion it is of interest that in this experiment there was a depression of ipsilateral flexion when evoked 1 second after a contralateral flexion-reflex. This depression was greater the longer the duration of the preceding contralateral flexion-reflex was ; and it was also found that the augmentation of contralateral flexion after an ipsilateral flexion-reflex (as here figured) was greater the longer the duration of the preceding ipsilateral flexion-reflex was.

This figure demonstrates an instance in which the immediate effect of double stimulation was flexion of smaller extent than in the "pure" ipsilateral reflex, but of greater extent than in the "pure" contralateral flexion-reflex.

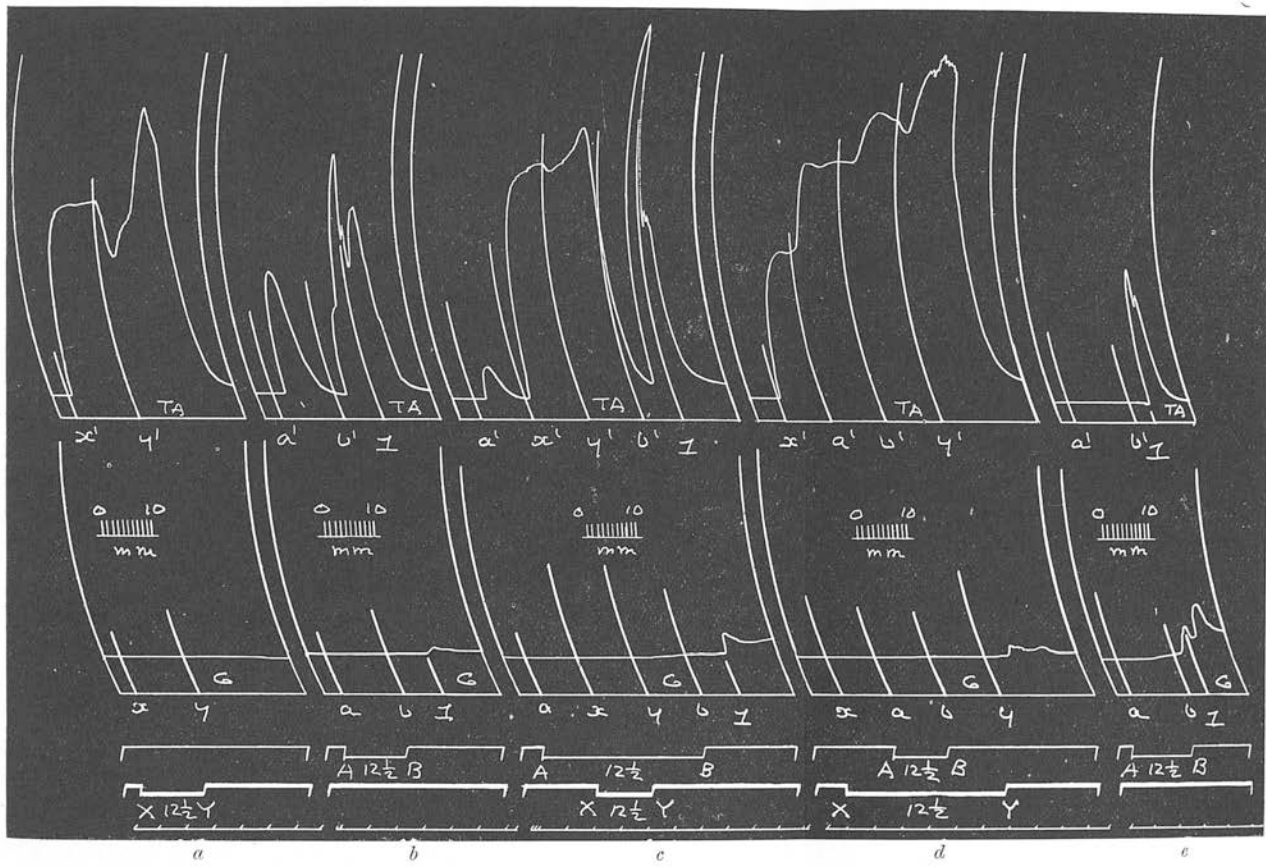


FIG. 28.—Experiment C, clviii., record 283, 6828 ; 11/2/13.—Decerebrate cat. A series of five reactions taken at minute intervals 1 hour and 54 minutes after decerebration, and exhibiting the effect of the compounding of a normal ipsilateral flexion-reflex and an abnormal contralateral flexion-reflex.

Reaction *a* is a "pure" ipsilateral flexion-reflex of "spinal" type. Note the "flexor rebound contraction after excitation."

Reaction *b* is a "pure" abnormal contralateral flexion-reflex. The flexor contraction dies during the short period of stimulation. Note the flexor rebound contraction, which is broken by a relaxation phase. There is a slight reciprocal extensor rebound contraction at ordinates 1.

Reaction *c* is a compound one with a "background" of abnormal contralateral flexion. Note that during double stimulation (ordinates *x*, *x'*–*y*, *y'*) there is marked increase of flexor contraction, which attains a level greater than in the "pure" ipsilateral reflex ; compare with *a* and with the first part of reaction *d* (ordinates *x*, *x'*–*a*, *a'*). On withdrawal of the ipsilateral stimulus there is, in the third phase of the compound reaction (*y*, *y'*–*b*, *b'*), a still further increase in the level of flexor contraction, reminiscent of the flexor rebound contraction in *a* ; and on withdrawal of the contralateral "background" stimulus there is a flexor rebound similar to, but of greater extent than, that in *b*.

Reaction *d* is another compound one with a "background" of ipsilateral flexion. Here there is flexor augmentation during double stimulation, and a further augmentation in the third phase of the reaction. Finally, withdrawal of the ipsilateral "background" stimulus is followed by a flexor rebound contraction which is greater than in the "pure" ipsilateral reflex.

Reaction *e* is a final "pure" contralateral reflex. There is now no flexor contraction during stimulation. There is a very slight extensor contraction.

This figure illustrates the augmentation of flexion—even to a level greater than in the "pure" ipsilateral flexion-reflex—which is sometimes obtained during double stimulation.

relaxation of flexor contraction which brought the curve of that muscle below the level of the maintained contraction of the "pure" ipsilateral flexion-reflex. Synchronously with the period of the augmenting flexor contraction there was an extensor relaxation, and when the flexor began to relax there was a reciprocal phase of extensor contraction. This gradually increased during the remaining portion of the period of double stimulation, and actually became greater in extent than the extensor element of contraction in the "pure" contralateral reaction obtained at the same strength of contralateral stimulation one minute before.

In another instance the effect of compounding the ipsilateral flexion-producing stimulus and the contralateral stimulus—which in this case gave abnormal flexion uncomplicated with extensor contraction—was to give summation of the two. In this instance a subliminal ipsilateral stimulus was first applied, and during its application a contralateral stimulus which gave a small flexor contraction when applied alone was added. The resultant reaction during the period of double stimulation was one in which the flexor contraction was very much greater than in the "pure" reaction of contralateral flexion. A subliminal contralateral stimulus was then applied within the period of a subliminal ipsilateral stimulus, and during the period of double stimulation there was a marked flexor contraction. Still using this subliminal contralateral stimulus, the strength of the subliminal ipsilateral stimulus was reduced in successive reactions, and the extents of the flexor contraction conditioned during the periods of double stimulation in these were found progressively to be decreased. In a following series two subliminal antagonistic stimuli were kept of constant strength but, the ipsilateral being first applied, the interval of time between its commencement and that of the contralateral stimulus was progressively lengthened. It was then found that the extent of the flexor contraction conditioned during the period of double stimulation was greater the later the contralateral stimulus was applied within the limit of a period of two seconds between the commencements of the two stimuli. When the contralateral stimulus was commenced three seconds after the commencement of the ipsilateral the flexor contraction during double stimulation was found again to be less.

In other experiments in which there was a contralateral flexion-reflex there has also been observed to be a summation of flexion, unaccompanied by extensor contraction, during double stimulation against an ipsilateral "background" (fig. 28).

## VIII. Phenomena in the De-afferented Condition.

### A. Stimuli of Asynchronous Commencement—Contralateral Extension-Reflex preceding Ipsilateral Flexion-Reflex.

The experiments with de-afferented preparations confirm those in which the preparations were normal as concerns the proprioceptive arcs of the

muscles the movements of which were recorded. In the period of double stimulation both the flexor and the extensor contractions are smaller than in the "pure" ipsilateral or contralateral reactions. When the ipsilateral flexion-producing stimulus is applied during the application of the contralateral extension-producing stimulus there is conditioned a state of extensor relaxation. This, as before, in extent varies with the strength of the interfering ipsilateral stimulus. Where that is comparatively weak there is a comparatively small relaxation of the extensor, while there may be no reciprocal flexor contraction, although a marked one may accompany the application of the same ipsilateral stimulus when given alone. With a stronger ipsilateral stimulus there is a greater extensor relaxation; and this may be accompanied reciprocally by a flexor contraction—which, however, is of less extent than the flexor contraction of the "pure" ipsilateral flexion-reflex evoked at the same strength of stimulus.

In one experiment an interesting series in which the interfering ipsilateral stimulus (flexion) was kept of constant value, but in which the "background" stimulus was progressively increased in value, was obtained. Here the progressive increase in the strength of the contralateral stimulus gave a small increase in the extent of extensor contraction in succeeding reactions. The ipsilateral stimulus was applied in each case two seconds after the commencement of the contralateral. When the contralateral stimulus was comparatively weak (although it then evoked an almost maximal reaction of extensor contraction), the ipsilateral stimulus conditioned a marked relaxation of the extensor and a marked flexor contraction. As the strength of contralateral stimulation was successively increased the ipsilateral stimulus conditioned in the period of double stimulation an ever smaller degree of extensor relaxation and of flexor contraction. Finally, these were almost minimal.

In these experiments it was noticed that there seemed to be a greater tendency than in the ordinary decerebrate preparation for the complete suppression of the flexor contraction element which would otherwise have been conditioned by the ipsilateral stimulus. That is to say, that an ipsilateral stimulus, which evoked a good reaction of flexor contraction when given alone, would, when applied during the period of a contralateral stimulus, give no flexor contraction; whereas a stimulus which evoked an equivalent reaction in the normal preparation would have been expected to do so. This is of interest inasmuch as, although complete suppression of flexor contraction might occur during double stimulation, yet if then the contralateral stimulus was withdrawn—leaving the ipsilateral in action—there might occur a great flexor contraction as a successive effect of double stimulation. The flexor may, in such cases, attain a level of contraction much greater than in the "pure" ipsilateral flexion-reflex—and this although no rebound phenomena occur in the "pure" reflexes.

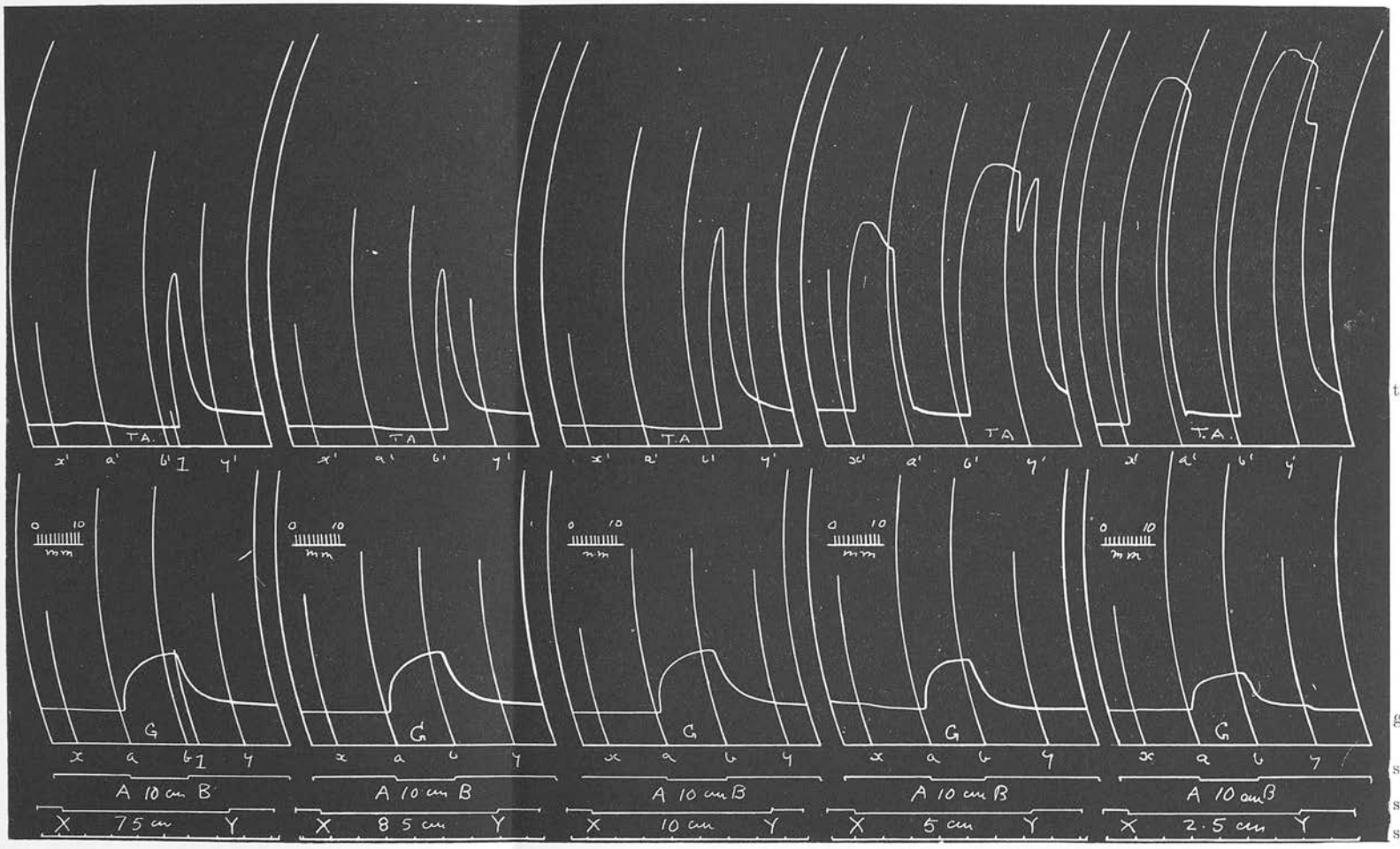


FIG. 29.—Experiment C, xlvi., record 80, 1964 ; 8/6/11.—Decerebrate cat, de-afferent condition. A series of reactions taken at minute intervals 7 hours and 12 minutes after decerebration.

In this series the interrupting contralateral stimulus is of constant strength, but the value of the "background" ipsilateral stimulus is progressively increased in the separate reactions. Note that in every case there is a complete (or nearly complete) relaxation of flexor contraction during double stimulation—even in *e*, where the value of the ipsilateral flexion is high. Note also that, although this depression of flexion in every case is complete, there is yet a certain degree of grading in the reciprocal extensor contraction. Thus the extensor contraction during double stimulation in *a* is of greater extent than that in *e*. Note also the augmentation of flexor contraction in the third phases of the reactions (ordinates *b*, *b'–y*, *y'*). There is here an evident flexion augmentation as a successive effect of double stimulation. There was, however, in the "pure" contralateral extension-reflex a flexor rebound contraction. This was of comparatively small extent, and here it seems probable that there was in the third phase a summation of this with an augmentation of the effects of the ipsilateral stimulus.

Fig. 31 of the eleventh paper of this series (7) immediately follows upon this one. There reaction *a* is a "pure" contralateral extension-reflex obtained with the strength of contralateral stimulation here used. That figure shews a curious reversal of the "pure" contralateral reaction from extension to abnormal flexion. This is all the more remarkable in view of the very pronounced dominance of extension shewn in the above figure.

B. Stimuli of Asynchronous Commencement—Ipsilateral Flexion-Reflex preceding Contralateral Extension-Reflex.

Here, as in the "normal" condition, the general rule seems to be that the application of a contralateral stimulus during the period of application of an ipsilateral conditions a reciprocal relaxation of the flexor contraction accompanied by an extensor contraction, which, however, is smaller in extent than that of the extensor contraction in the "pure" contralateral reaction. The two antagonistic muscles reciprocally assume a state of algebraic summation between their states in the two separate reactions compounded. There seems here, however, to be also a greater tendency for the second stimulus completely to abolish the flexor contraction.

When the background stimulus of ipsilateral flexion is increased in strength in successive reactions, the effect of the interrupting contralateral stimulus is progressively reduced. The extensor contraction which it conditions and the flexor relaxation become smaller. If the interrupting contralateral stimulus be increased in value its effect becomes augmented. There is a greater flexor relaxation and extensor contraction. Where the contralateral stimulus is comparatively strong it may produce a complete relaxation of the flexor contraction even when the background ipsilateral stimulus is a fairly strong one. Thus with a contralateral stimulus of a certain strength even a maximal flexor contraction may give place to complete relaxation during the period of double stimulation. In one experiment (fig. 29) it was found that when the strength of contralateral stimulation was sufficient to give complete relaxation of the maximal flexor contraction of the ipsilateral flexion-reflex and, being kept constant, it was pitted against various values of the ipsilateral stimulation, each time it evoked a complete flexor relaxation, but the reciprocal extensor contraction was yet smaller the stronger the ipsilateral stimulus was.

As in the "normal" condition, the general rule of flexor relaxation and extensor contraction is not always held. It occasionally happens that there may be a flexor augmentation during the period of double stimulation.

This may be comparatively slight or it may be well marked, although not lasting throughout the whole period of double stimulation. In the best-marked example the augmentation of the flexor contraction of the ipsilateral flexion-reflex during the period of double stimulation was brief. It soon gave place to relaxation of flexor contraction, which carried the curve of the muscle far below the level of the "pure" flexion-reflex. There was no extensor contraction, and the strength of contralateral stimulation was comparatively weak.

In one experiment (fig. 30) the ipsilateral stimulus evoked a reaction characterised by a comparatively small flexor contraction and a very marked late extensor contraction and flexor relaxation—the flexion-reflex of "decerebrate" type (5, fig. 21). The contralateral extension-reflex at the same time could not be evoked at a certain strength of stimulus afterwards

used in a compounded reaction. A weak ipsilateral stimulus was then applied and evoked a slight flexor contraction followed by a marked

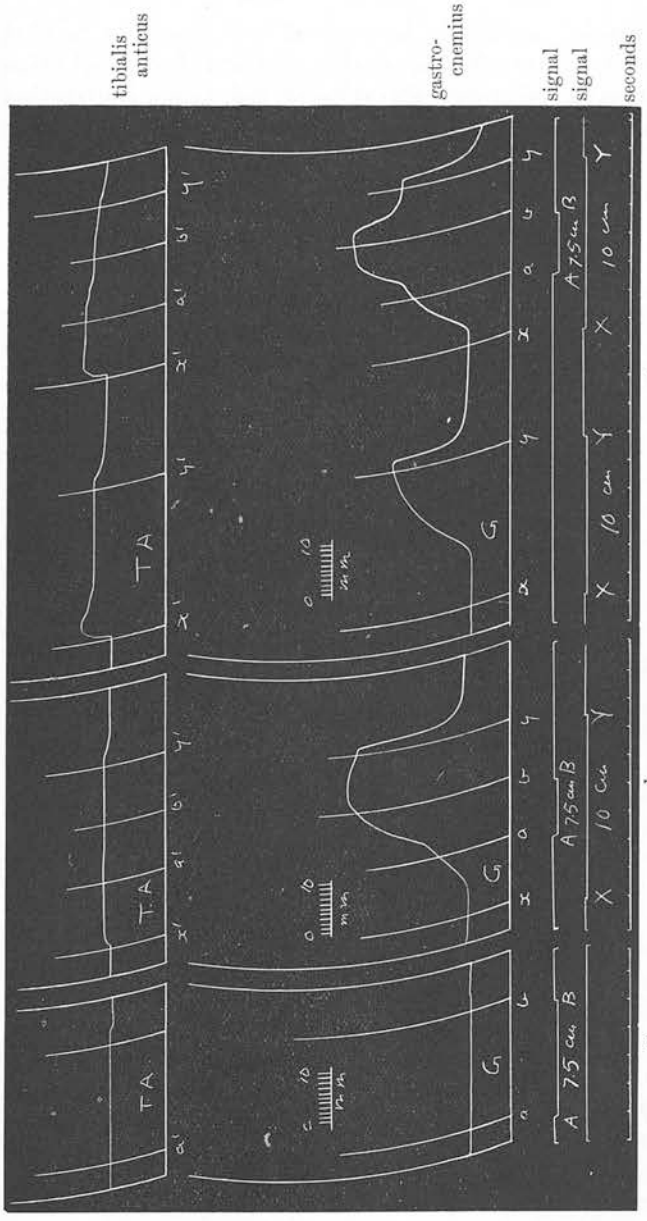


FIG. 30.—Experiment C, xlix., record 84, 2074; 16/6/11.—Decerebrate cat, de-afferented condition. A series of three reactions taken at 2-minute intervals 1 hour and 56 minutes after decerebration.

Reaction *a* is a subliminal contralateral one, the strength of stimulation being that used in the following reactions.

In reaction *b* this is compounded against a weak ipsilateral "background." The ipsilateral reaction is of "decerebrate" type, and during double stimulation there is an augmentation of extensor contraction. This augmentation is maintained in the third phase of the reaction.

In reaction *c* there is first applied a "pure" ipsilateral stimulus which evokes a flexion-reflex of "decerebrate" type. Then, after an interval of about 4 seconds, the two stimuli are again compounded as before—with the same results, but with the exception that here the extensor augmentation is not maintained in the third phase of the compound reaction.

In this case there is very evident a summation of the extensor contraction of the contralateral reflex and of the extensor contraction which appears here late in the flexion-reflex of "decerebrate" type.

extensor contraction. While this was in being the subliminal contralateral stimulus was applied, and at once produced a marked augmentation of the extensor contraction. On repeating this there was an even more distinct

increase of the extensor contraction during the period of double stimulation. Three hours later the phenomenon was still distinct.

## IX. Conclusions and Summary.

The present paper itself is the summary of a large number of experiments, and it is not possible again to refer to all the points described in it. The following may, however, be noticed:—

1. Where the two antagonistic stimuli are commenced synchronously, "algebraic summation" (Sherrington) of the two "pure" reflexes may occur in the compound reaction. In some cases, however, complete suppression of one—usually the extension-reflex—may occur. In such cases there may still be reduction of the extent of the contraction of the active muscle—for instance, the flexor.

2. Where the contralateral stimulus is applied first and allowed to run for a short period before the application of the interrupting ipsilateral stimulus, extensor relaxation occurs in the period of double stimulation, and this may or may not be accompanied by flexor contraction. The two may shew "algebraic summation," and the values of flexor contraction and extensor relaxation increase with increase in the strength of the ipsilateral flexion-producing stimulus, as well as with decrease in the value of the "background" contralateral extension-producing stimulus. Sometimes, however, the flexor contraction of double stimulation is actually greater than in the "pure" flexion-reflex.

3. When, in these circumstances, the temporal relations of the two stimuli are changed—so that the duration of the contralateral extension "background" before the commencement of double stimulation is varied,—it is found that often the extent of flexor contraction during double stimulation is greater the later the ipsilateral stimulus is applied. But at the same time the extent of extensor relaxation does not reciprocally increase—it usually shews progressive diminution of extent. In these experiments the duration of precurrent contralateral "background" has been varied within the limits of 0 seconds and 6 seconds.

4. When the ipsilateral stimulus is first applied the period of double stimulation which is conditioned by the addition of a contralateral stimulus is characterised by a reduction of the flexor contraction, and by the appearance of an extensor contraction which is smaller in extent than that of the "pure" contralateral extension-reflex.

5. If, in these circumstances, the strengths of the compounded stimuli are varied, it is found that the flexor relaxation is smaller in extent, and the extensor contraction also smaller the stronger the ipsilateral "background" is.

6. If the temporal relations of the two stimuli are altered—but the stimuli kept of constant value—it is found that the component of extension in double stimulation is greater the longer the ipsilateral stimulus is allowed to run before the commencement of double stimulation.

7. Flexor relaxation during double stimulation is not the invariable rule. Sometimes augmentation occurs. When this is the case it may increase in value with increase in the strength of the interrupting contralateral stimulus, and at the same time there may occur a reduction of extensor contraction during double stimulation. When the temporal relations of the two stimuli are altered the flexor augmentation may be found to increase with increase of duration of the first applied ipsilateral stimulus. But a maximum may be attained, after which diminution of flexor augmentation occurs with further increase in the duration of time which separates the commencement of the ipsilateral stimulus from the commencement of double stimulation.

8. If the effects of double stimulation are compared in cases in which the preceding "background" is flexion with the effects in cases in which that "background" is extension, it is found that the phenomena differ in the relative values of flexion and extension. Thus if a two-second flexion "background" precede double stimulation, there may be a greater degree of flexion and a lesser degree of extension in the summation phenomena of double stimulation as compared with the same components when a two-second extension "background" precedes the double stimulation. These differences may be referred to two conditioning factors. In the first place, the stimulus to be first applied ("background") tends to "hold the field" to the comparative exclusion of the other. In the second place, this "capture of the field" tends rapidly to deteriorate in value.

9. When two series of reactions, in which the preceding "background" is flexion and in which it is extension, are compared, it is found that when the duration of the "background" before the commencement of double stimulation is small, the first applied stimulus ("background") holds the field. Thus here there is a greater factor of flexion in double stimulation when the flexion-producing stimulus is the "background" and a greater factor of extension when the contralateral stimulus is first applied. With a greater duration of preceding "background" the factors of flexion and extension in double stimulation are similar whichever of the two stimuli is first applied. This may be termed the "neutral duration of preceding background." With still greater durations of preceding "background" the "background" stimulus no longer "holds the field." When these durations are used it is found that after a flexion "background" there is a greater extension factor in double stimulation than after an extension "background" of the same previous duration before the commencement of double stimulation.

10. Experiments in which the temporal relations of the two stimuli are kept constant, but in which their strengths are varied, seem to shew that the "capture of the field" is more complete, and lasts for a longer time in the period of a reflex, the stronger the evocative "background" stimulus.

11. Where the abnormal ipsilateral extension-reflex is compounded with

the normal contralateral extension-reflex there may be augmentation of extensor contraction during double stimulation—so that the level attained is greater than that in either of the compounded reflexes. This result is seen usually when the ipsilateral stimulus is very weak. The extensor contraction during double stimulation may even be greater in extent than the sum of the extents in the "pure" reflexes. Where the ipsilateral stimulus is relatively stronger the extensor contraction during double stimulation may be the mean of the extensor contractions in the two "pure" reactions. Where still stronger—even where the "pure" ipsilateral reaction is still one of extension alone—the extensor contraction during double stimulation may be smaller in extent than this mean.

12. Where the extensor contraction during double stimulation in these abnormal cases is compared when the preceding "background" is the ipsilateral extension with that when the preceding "background" is contralateral extension, it is found that with weak ipsilateral stimuli there is a greater extensor contraction against the ipsilateral "background" than against the contralateral. With stronger ipsilateral stimuli there may be equal extents in the two cases. With yet stronger ipsilateral stimuli there may be less extensor contraction during double stimulation against the ipsilateral "background" than against the contralateral. As in these experiments the duration of the preceding "background" stimulus was kept constant, this seems to mean that with weak ipsilateral stimuli which give the abnormal direct extension-reflex, the preliminary phase of flexion (not directly evidenced), if it occurs at all, is of short duration. In other words, the "neutral duration of preceding background" is very small—perhaps infinitely small—and thereafter the extension factors tend increasingly to "hold the field." As the strength of ipsilateral stimulation is increased the primary flexion "capture of the field" either appears or, if previously present, increases in duration. The "neutral duration of preceding background" therefore increases, and the fixed duration of preceding "background" used in the experiments may coïncide with this—when the extension value of double stimulation will be the same for the two "backgrounds." With still stronger ipsilateral stimuli the period of double stimulation may fall in the preliminary phase in which flexion (there directly evidenced in the stronger ipsilateral reflex) "holds the field." In such cases the extensor contraction during double stimulation will be weaker against the ipsilateral "background" than against the contralateral.

13. Sometimes when the preceding "background" is contralateral extension, and even where the "pure" ipsilateral stimulus evokes extensor contraction alone, there may appear flexor contraction during double stimulation. In such cases the presence of the contralateral "background" seems actually to reverse the ipsilateral reaction from abnormal extension to normal flexion. Related to this are the cases in which extensor relaxation unaccompanied by flexor contraction occurs during double stimulation.

A possible explanation of this phenomenon is that the "neutral duration of preceding background" having been passed in the contralateral reflex, the latent flexor element of the ipsilateral reaction was augmented by the contralateral extension "loss of the field."

14. Where an abnormal contralateral flexion-reflex occurs and is compounded with a normal ipsilateral flexion-reflex, there appears usually flexor augmentation during double stimulation. Two subliminal stimuli when compounded in these circumstances may give a flexion reaction. If the preceding "background" is contralateral flexion, the flexor contraction during double stimulation is most often of smaller extent than that in the "pure" ipsilateral flexion-reflex. But sometimes it is larger. When the ipsilateral stimulus is first applied there occurs most often flexor agumentation during double stimulation. It is possible that in such experiments the "neutral duration of preceding background" is comparatively great for the flexion-reflex; that is to say, that flexion "holds the field" for a longer time than is usual.

15. In de-afferented conditions the immediate phenomena of compound stimulation correspond to those in "normal" conditions. When the contralateral stimulus is first applied there occurs extensor relaxation and flexor contraction during double stimulation. These decrease in value with decrease in the relative strength of ipsilateral stimulation. It has been observed that there seems to be a greater tendency in de-afferented conditions than in "normal" for a complete suppression of flexor contraction during double stimulation.

16. Where, in the de-afferented condition, the ipsilateral stimulus is first applied, there is often the usual phenomenon of algebraic summation during double stimulation. Here again there seems to be a greater tendency than in the "normal" condition for complete flexor suppression to occur during double stimulation. In such cases, when the strength of contralateral stimulation is relatively increased, there may yet appear grading of the extent of extensor contraction during double stimulation although there is in every case complete flexor suppression. Sometimes, as in "normal" conditions, there may occur flexor augmentation during double stimulation. This usually is transient, and does not persist throughout the whole of the period of double stimulation. Where approximations to the abnormal direct extension-reflex have occurred there has been observed to be extensor augmentation during double stimulation.

17. This phenomenon of flexor suppression is one of interest because it might have been supposed that the reverse would be the case. Thus in the period of double stimulation against an extension "background" the extension-reflex is relatively depressed, and in the "normal" condition it may be supposed that in this period there is in being some factor which corresponds to the extensor after-discharge of the "pure" extension-reflex. In this phase there will thus be a compounding of one flexion factor with two extension factors. But in the de-afferented condition this extensor

after-discharge is almost completely suppressed. It would therefore be supposed that de-afferented conditions would demonstrate a greater extensor relaxation during double stimulation than "normal" conditions when the "background" is one of contralateral extension. In a similar manner there might be supposed to occur a less flexor relaxation during double stimulation against a flexion "background" in de-afferented than in "normal" conditions—because in the "normal" condition there most often follows upon flexion suppression in the "pure" reflex an extensor rebound of maintained form, and this does not occur, or is more transient, in the de-afferented condition.

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STUDIES IN THE PHYSIOLOGY OF THE NERVOUS SYSTEM. XVI.: DECEREBRATE PREPARATIONS, SUCCESSIVE PHENOMENA IN COMPOUND REACTIONS—STIMULI OF SYNCHRONOUS TERMINATION AND STIMULI OF ASYNCHRONOUS TERMINATION WHERE THE EXTENSION-REFLEX IS LEFT IN ACTION. By T. GRAHAM BROWN (Manchester). (With twenty-two figures in the text.)

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# STUDIES IN THE PHYSIOLOGY OF THE NERVOUS SYSTEM. XVI.[1]: DECEREBRATE PREPARATIONS, SUCCESSIVE PHENOMENA IN COMPOUND REACTIONS—STIMULI OF SYNCHRONOUS TERMINATION AND STIMULI OF ASYNCHRONOUS TERMINATION WHERE THE EXTENSION-REFLEX IS LEFT IN ACTION.

By T. GRAHAM BROWN (Manchester).[2] (With twenty-two figures in the text.)

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CONTENTS.



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## I. Introduction.

A reflex stimulus upon withdrawal is often followed by movements of the antagonists—the movements being of a somewhat different nature to those which occur during the period of reflex stimulation. These "terminal reflex phenomena" ("rebound" or "successive reflex phenomena") have already been described in some detail in a previous paper in this series. Sometimes the contractor of the reflex reaction exhibits an augmentation of contraction on withdrawal of the exciting stimulus (flexor or extensor "rebound" [or "terminal," or "successive"] contraction after excitation). Sometimes (and more often) the relaxor of the reflex reaction exhibits a phase of contraction on withdrawal of the exciting stimulus (extensor or flexor "rebound contraction after inhibition"). These acts of contraction are commonly accompanied by reciprocal relaxation of the muscles antagonistic to those which exhibit the rebound contraction — rebound relaxation after contraction or after inhibition,—and this relaxation may be exhibited even where there is no evident rebound contraction. Rarely rebound contraction is seen synchronously in the two antagonists.

Whatever be the meaning of these reflex terminal phenomena, it is clear that they present an interesting problem in connexion with the study of reflex compound reactions.

Thus it may be supposed that in the contralateral extension-reflex there is a flexor rebound contraction upon withdrawal of the exciting stimulus. In such a case the question naturally presents itself, whether or no there is a modification of this rebound contraction when an ipsilateral stimulus is applied and terminated synchronously with the application and termination of the contralateral. Or again, how the rebound behaves

when the strength of the ipsilateral stimulus is varied. And yet again, how it behaves when the duration of the ipsilateral stimulus before the period of double stimulation (the stimuli here not being synchronously commenced) is varied.

And when the compounded stimuli are not synchronously terminated —but when the "background" stimulus is carried on after the period of double stimulation—other, and as interesting, problems arise. Thus—is a flexor rebound contraction after the contralateral extension-reflex altered if the course of that reflex is interrupted by an ipsilateral stimulus? If so, how is this variation altered by changing the strength of the interrupting stimulus? And how is it altered by altering the duration of continuation of the "background" after the period of double stimulation?

In such compound reactions in which the "background" stimulus is continued after double stimulation, other problems are presented in connexion with the behaviour of the "background" reaction after the close of the period of double stimulation. Here there is in reality a compounding of an "immediate" reflex reaction (the "background" reflex) with a "terminal" reflex reaction (the terminal effect of the interrupting stimulus). In this phase of the compound reaction it is possible that either depression or exaltation of the "background" reaction might occur as a terminal (or "successive") effect of the interrupting stimulus. Or again, where the interrupting stimulus is itself followed by positive terminal phenomena, there is here a compounding of a rebound phenomenon with an immediate reflex phenomenon. And all these possibilities present problems of interest in the study of successive compound reflex phenomena. These phenomena, in as far as they occur in spinal preparations, have been noticed in a previous paper, but to the best of my knowledge no great attention has as yet been paid to this subject.

It is obvious that the subject is a very large one, and the mass of experimental material necessary to cover it—even imperfectly—great. In order to present the phenomena in as manageable a manner as possible, I have confined the present paper to a small part only of the subject—successive phenomena after double stimulation of synchronous termination of stimuli, and successive phenomena where there is asynchronous termination of the stimuli and the continued "background" is contralateral extension. For convenience, although the distinction is perhaps arbitrary, each of these kinds of successive phenomena is here discussed separately for experiments in which there were no rebound phenomena in the "simple" reflexes (save of course rebound relaxation after the flexion-reflex) and for experiments where terminal rebound phenomena occurred. In the following papers of this series it is intended to discuss the successive phenomena where the continued "background" is one of ipsilateral flexion, where the reactions are abnormal (ipsilateral extension or contralateral flexion), and where the antagonists are de-afferented.

Before passing to the experimental part of the paper a word may be said

about the terminology here used. In the compound reactions it has been most usual to commence one stimulus before, and terminate it after, the other stimulus. In such an arrangement of stimuli that which is first commenced and last terminated is called the "background" stimulus. The other is called the "interrupting" stimulus, or the "interruptor." This arrangement of stimulation naturally divides the compound reaction into four chief phases. Of these the first phase is that in which the "background" stimulus runs uncompounded before the application of the "interruptor." In this phase the reflex phenomena are "simple" or "pure" immediate reflex phenomena—similar to those examined in the eleventh paper of this series. The second phase of the compound phenomenon is that in which the interrupting stimulus is in being against the continued "background" stimulus. This is the period of double stimulation, and the phenomena presented are "immediate reflex compound phenomena," and as such have been described for decerebrate preparations in the fifteenth paper of this series. The third phase of the compound phenomenon is that which commences at the point of withdrawal of the interrupting stimulus and lasts during the continuation of the "background" stimulus —terminating with the withdrawal of the "background" stimulus. Here the reflex phenomena are "successive (or terminal) reflex compound phenomena," and are conditioned by the compounding of the terminal effects of the interrupting stimulus with the immediate effects of the "background" stimulus. The fourth phase of the compound phenomenon is that which follows the withdrawal of the "background" stimulus. It lasts until the centres again resume the condition of "rest," and in it there occur the ordinary terminal phenomena of the "background" stimulus modified by the precurrent interrupting stimulus.

## II. Methods Employed.

The methods employed in the present experiments were the same as those described in previous papers in this series. The animals (cats) were unconscious throughout the experiment from its commencement and until they were destroyed at its termination.

## III. Successive Phenomena in Compound Stimulation: Stimuli of Synchronous Termination where there are no Rebound Contractions as Terminal Phenomena present in the Simple Reflexes.

When two antagonistic stimuli are simultaneously compounded and synchronously terminated the successive effects of the double stimulation may possibly differ from the successive effects of either of the two stimuli when applied uncomplicated by the other. Such a difference might be evident either in a change in the after-discharge of the activated muscles,

or in a change in the "rebound" phenomena when these are present. In this section the conditions are considered in decerebrate preparations in which there was no "rebound" phenomena of contraction, and in which the terminal phenomena consisted of flexor relaxation after the flexion-reflex ("flexor terminal relaxation after excitation"); and, after the extension-reflex, either extensor relaxation or a tonic extensor after-discharge (which may possibly be looked upon as due to a delayed "extensor terminal relaxation after excitation").

Even where there is an extensor tonic after-discharge in the contralateral extension-reflex, this may be completely suppressed after the synchronous termination of the same contralateral stimulus and an antagonistic ipsilateral stimulus of sufficient strength. This seems to occur when the strength of ipsilateral stimulation is sufficient completely to suppress any element of extensor contraction during the period of double stimulation (fig. 1). In such a case there may be (as compared with the "pure" flexion-reflex) no evident change in the rate of relaxation of the flexor muscle on the termination of the period of double stimulation.

If the comparative difference in strength of the two stimuli is smaller than this—so that there is an element of extensor contraction during the phase of double stimulation—the extensor after-discharge may be cut short. In such a case the course of events may be described as follows:—During the period of double stimulation the flexor first contracts (but not to the extent seen in the "pure" flexion-reflex evoked with the same strength of ipsilateral stimulation). It then begins to relax, and at the same time the extensor begins to contract. If the period of double stimulation be one of 4 seconds, let us say, the flexor relaxes gradually during the further course of stimulation, and the extensor contracts. At the termination of double stimulation the extent of flexor contraction is at its smallest, and that of extensor contraction is at its greatest; neither is as great as in the respective "pure" reflexes. After the termination of the period of double stimulation the flexor at once begins to relax to the level of rest, but the extensor may remain in maintained contraction for as long as 1 second. It then rapidly relaxes also to the position of rest. The terminal fall of the extensor is then much more rapid than in the "pure" extension-reflex—in which the extensor after-discharge of maintained contraction lasts for many seconds and dies gradually away [see xv. fig. 11].

In an experiment in which this was observed the contralateral stimulus, in a series of reactions, was first applied at an ever greater length of time after the commencement of the ipsilateral flexion-producing stimulus; after 4 seconds of double stimulation both stimuli were terminated. It was then found that the extensor after-discharge became more pronounced and of longer duration the later in the flexion-reflex the contralateral stimulus was applied. When the interval of time which separated the commencements of the two stimuli was comparatively great, the extensor after-

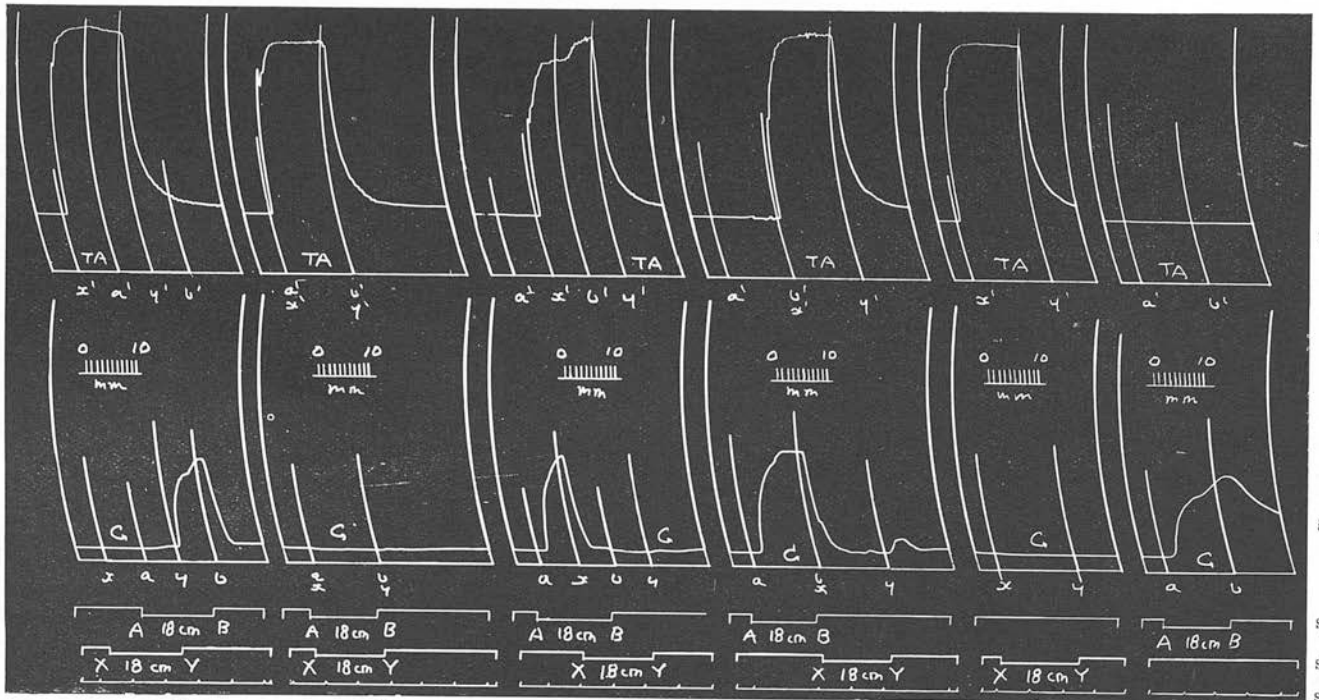


FIG. 1.—Experiment C, clxiii., record 261, 6126; 2/11/12.—Decerebrate cat. A series of reactions obtained 1 hour and 50 minutes after decerebration, at intervals of 1 minute.

Reaction *e* is a "pure" flexion-reflex. Reaction *f* is a "pure" extension-reflex. In it there is an after-discharge which, however, is not well sustained; there is also indication of a slight "extensor rebound contraction after excitation." In the flexion-reflex there is no positive rebound phenomenon.

In reaction *a* the stimuli are in "step" arrangement. The ipsilateral is first applied, then the contralateral is added, then the ipsilateral is withdrawn and the contralateral continued. During the period of double stimulation (ordinates *a*, *a'*-*y*, *y'*) there is little flexor relaxation, and almost complete extensor suppression. On withdrawal of the ipsilateral stimulus there is extensor contraction, and on withdrawal of the contralateral stimulus there is a much sharper relaxation of the extensor than in the "pure" extension-reflex.

In reaction *b* the two stimuli are applied and terminated synchronously. During double stimulation there is no element of extensor contraction, and no extensor contraction occurs after its termination.

In reaction *c* the stimuli are again in "step" arrangement, but here the contralateral is first applied and first withdrawn. During double stimulation there is nearly complete extensor relaxation, and on withdrawal of the contralateral stimulus increase of the flexor contraction occurs. When the ipsilateral stimulus is finally withdrawn there is a very slight extensor contraction.

In reaction *d* the two stimuli are applied in temporal succession—contralateral leading. On withdrawal of the ipsilateral stimulus there is a greater extensor rebound contraction. [In a previous reaction in which the temporal succession was in the reverse order there occurred a sharp extensor relaxation on withdrawal of the contralateral (last) stimulus, and this was accompanied by a flexor rebound contraction.]

discharge died slowly away as in the "pure" extension-reflex [see xv. figs. 2, 3].[1] If stronger ipsilateral stimuli were used, or if the contralateral stimulus was first applied and the ipsilateral stimulus applied late in the period of the extension-reflex, the extensor suddenly relaxed on termination of the double stimulation [see xv. fig. 3].

## IV. Successive Phenomena in Compound Stimulation: Stimuli of Synchronous Termination—Rebound Contractions present as Terminal Phenomena in the Simple Reflexes.

### A. Flexor Terminal Contraction Present.

If a flexor "rebound" contraction follow the termination either of the ipsilateral flexion-reflex or of the contralateral extension-reflex, that may be changed in extent when the two antagonistic stimuli (ipsilateral and contralateral) are synchronously compounded and synchronously terminated.

#### 1. Flexor Rebound Contraction in the Contralateral Extension-Reflex.

Thus in one experiment there was a well-marked flexor rebound contraction on cessation of the contralateral extension-producing stimulus. The ipsilateral stimulus with the strengths used was ineffective. But when the two stimuli were applied together, and synchronously terminated, the flexor rebound contraction was markedly smaller in extent than in the "pure" extension-reflex evoked at the same strength of contralateral stimulation. But here an interval of 14 minutes separated the two reactions compared, and the state of the centres may have changed—as later in the same experiment an augmentation of the flexor rebound after synchronously terminated double stimulation was observed. In that instance the "pure" contralateral reaction and the compound one compared with it were separated by an interval of 2 minutes of time.

In other cases augmentation of the flexor rebound has been observed. Thus in one experiment there was a very slight flexor rebound contraction on cessation of a "pure" contralateral extension-reflex which had run for 6 seconds. If the same stimulus was repeated but compounded during the last 2 seconds with a weak ipsilateral stimulus (the two being synchronously terminated), there was, on cessation of double stimulation, a very marked flexor rebound contraction which consisted of two beats. The weak "pure" ipsilateral reflex had no flexor rebound. In another case a strong extension-reflex was followed by a marked flexor rebound; and this, in its turn, by

[1] In each of these papers there must necessarily be cross-references to figures in some of the others. For convenience, in these references the number of the paper in the series is given in roman numerals, and the number of the figure of that paper referred to then follows. Thus the reference above means:—"See figures 2 and 3 in the fifteenth paper of this series"—that is, in the paper immediately preceding the present one.

a maintained extensor rebound. A strong ipsilateral reflex gave no flexor rebound, but a slight maintained extensor rebound. The two were then compounded for 2 seconds with synchronous commencement and termination, and on cessation of double stimulation there was a flexor rebound greater than that in the "pure" extension-reflex. This was followed by a smaller flexor rebound, and that by a tonic (or "maintained") extensor contraction of about the same extent as that in the "pure" extension-reflex (fig. 2). In this case it was of additional interest that the flexion-reflex often exhibited a marked flexor after-discharge. When the extension-reflex was applied "pure," but very soon after the flexion-reflex, the contralateral stimulus evoked flexion—not extension. This was observed to occur when the contralateral stimulus was commenced 0 second, 1 second, 2 seconds, and 3 seconds after the termination of the ipsilateral. The abnormal flexion effect was greater the sooner after the termination of the flexion-reflex the contralateral stimulation was commenced. It was not due to an "accidental" reversal—because on several occasions "pure" contralateral reactions were evoked 1 minute before and 1 minute after the reversed reactions, and in these circumstances gave the ordinary extension-reflex. In these reversed reactions there were flexor rebound contractions greater than in the "pure" extension-reflex. The rebound was of greater extent the sooner the contralateral stimulus was given after the termination of the ipsilateral. It must be remarked that, although at this time the "pure" contralateral stimulus evoked extension alone, earlier in the experiment abnormal crossed flexion reactions were recorded.

### 2. Flexor Rebound Contraction in the Ipsilateral Flexion-Reflex.

In another experiment the cessation of a "pure" ipsilateral stimulus was followed, as regards the flexor muscle, by relaxation—but about 1 second after termination of stimulation there was a large flexor rebound contraction. On then applying this ipsilateral stimulus synchronously with a contralateral extension-producing stimulus, there was, on cessation of the double stimulation, a continuation of the extensor contraction which had appeared during the phase of double stimulation. This lasted for about 1·3 seconds—the flexor had at once relaxed—and the extensor then suddenly relaxed. About 1 second after this there appeared a flexor rebound contraction of less than one-third the extent of the flexor rebound of the "pure" flexion-reflex. In this instance not only was the flexor rebound contraction reduced in height, but it was also very markedly delayed in its appearance. When it disappeared the state of maintained extensor contraction was again partially reëstablished. If the flexion-reflex was commenced in time before the beginning of the double stimulation, the rebound contraction did not appear at all. In this case there was

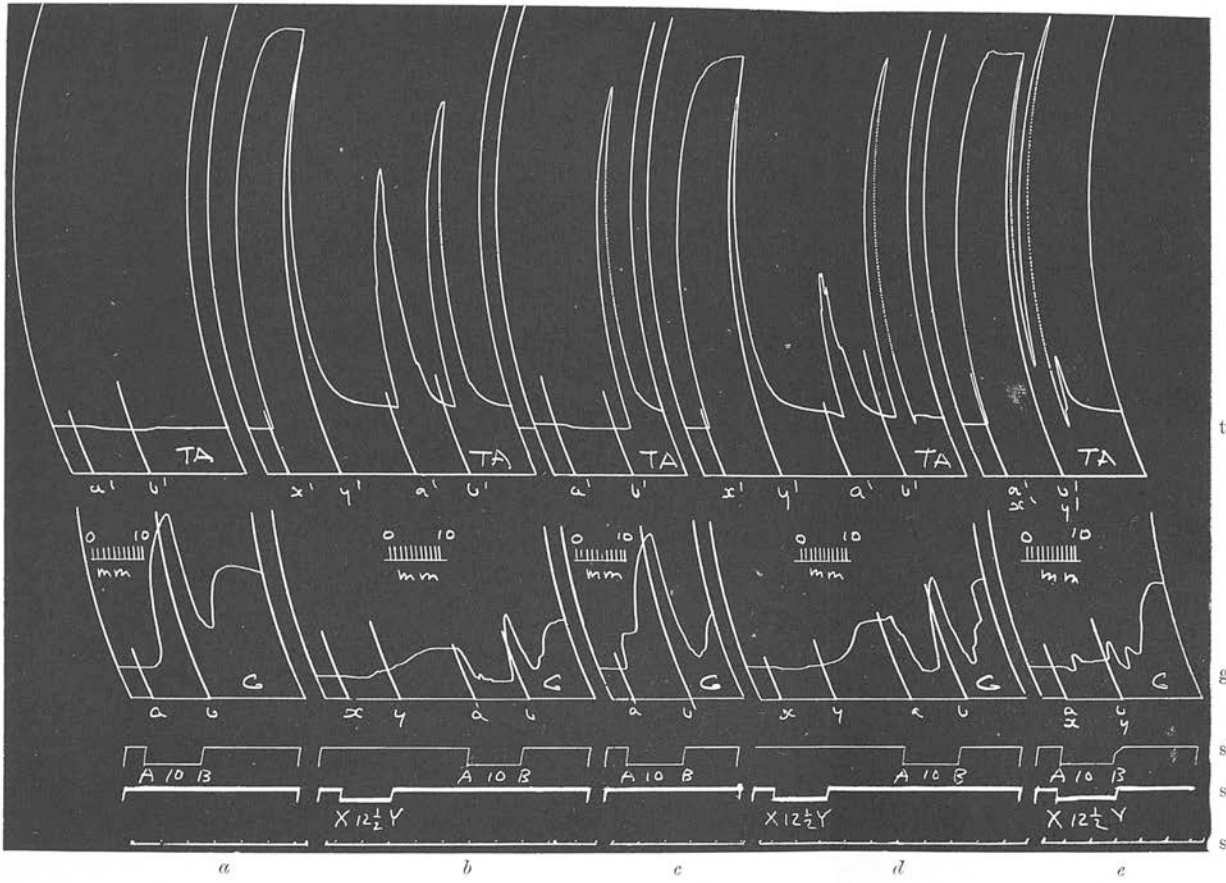


FIG. 2.—Experiment C, clxxv., record 316, 8511; 9/5/13.—Decerebrate cat (Manx); a series of reactions obtained 2 hours and 30 minutes after decerebration, minute intervals between reactions.

Reactions *a* and *c* are "pure" contralateral extension-reflexes. In *a* note the absence of flexor rebound contraction (or the extremely slight flexor rebound), and the presence of partial extensor relaxation followed by a reconstitution of the extensor after-discharge. In *c* note the presence of flexor rebound, the greater extensor relaxation, and the slower reconstitution of the extensor after-discharge. Also note the "step" in the extensor contraction during stimulation, and the shorter latency as compared with *a*.

The first parts of reactions *b* and *d* give "pure" flexion-reflexes. These are not followed by flexor rebound, but by an extensor rebound of slow constitution.

In reaction *b* a contralateral stimulus is made to follow an ipsilateral in temporal succession at an interval of about 3 seconds. It evokes flexor contraction followed by late extensor contraction during stimulation. Cessation of contralateral stimulation is followed by extensor relaxation and a marked flexor rebound. This is much larger than that in *a* (if there is one there) but smaller than that in *c*. This is again followed by a reconstitution of extensor after-discharge which is smaller than that in *a* or *c*.

Reaction *d* is similar to *b*, but here the flexor rebound after the contralateral stimulus is greater than that in *c*, and the reconstitution of extensor after-discharge is also greater.

Reaction *e* is one in which the two stimuli are synchronously compounded. Here cessation of stimulation is followed by flexor relaxation. This at once passes over into contraction in a flexor rebound which brings the level of flexor contraction above that which obtains in the "pure" flexion-reflex. It is greater in extent than that of the "pure" extension-reflex (*c*). This is followed by an extensor rebound similar to the reconstituted after-discharge of the "pure" extension-reflex.

This experiment seems to demonstrate the augmentation of a flexor rebound in a compounded reaction where the stimuli are synchronously terminated; and it gives a curious example of the reversal of a contralateral extension-reflex to an abnormal contralateral flexion-reflex when the contralateral stimulus follows an ipsilateral in comparatively close temporal succession.

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a marked extensor after-discharge in the "pure" extension-reflex [see xv. fig. 2].

In another case the same effect was seen. Here a "pure" ipsilateral stimulus, when applied for a period of 6 seconds, was followed on cessation by a marked "flexor rebound contraction after excitation." If, however, it was compounded during the last 2 seconds with a contralateral stimulus (which when "pure" gave the extension-reflex) there was, on synchronous termination of the two stimuli, a smaller flexor rebound. This was of about half the extent of that in the "pure" ipsilateral reflex. There was no flexor rebound with a weaker ipsilateral stimulus of 2 seconds' duration; and when this was applied during the last 2 seconds of a contralateral extension-reflex of 6 seconds' duration there was also no flexor rebound. In this experiment, as in one described above, there had previously been an abnormal flexion response to the contralateral stimulus, and a similar reversal to flexion of the extension-reflex when evoked very soon after the termination of a direct flexion-reflex was later observed. When the flexor rebound phenomenon here described was examined the "pure" extension-reflex was of "spinal" form in its immediate phase and was followed by a tonic extensor after-discharge. After the flexor rebound of the "pure" flexion-reflex there was also a marked maintained extensor discharge. In the compound reaction there followed, on cessation of double stimulation, firstly, the reduced flexor rebound, and secondly, a maintained extensor discharge of a smaller height than that in either of the "pure" reflexes. It must be noted, however, that later in the experiment both the flexor rebound and the extensor discharge were greater in the compound reaction than in the "pure" flexion-reflex.

Augmentation of a flexor rebound after double stimulation was more clearly seen in another instance. Here in the "pure" ipsilateral flexion-reflex there was a very slight flexor rebound followed by a maintained extensor discharge. In the "pure" contralateral extension-reflex there was no rebound and little extensor after-discharge — although the extensor contraction during stimulation was marked. When the ipsilateral stimulus was applied for 6 seconds and compounded during the last 2 seconds with a contralateral stimulus there was, on synchronous termination of the two stimuli, a marked flexor rebound contraction. This was not followed by a maintained extensor discharge. In this case it was remarkable that when the ipsilateral stimulus was allowed to continue in being after double stimulation the flexor rebound was smaller the longer the ipsilateral stimulus ran. When, on the other hand, the contralateral stimulus was continued, the rebound followed on the cessation of that stimulus. When the contralateral stimulus was commenced immediately on cessation of an ipsilateral, termination of the contralateral was followed by a flexor rebound—although that was not present in the "pure" extension-reflex. Similar results were obtained when the "background" was extension. The "pure" flexion-reflex of 2 seconds' duration gave an extensor rebound—no

flexor. The "pure" extension-reflex applied for 6 seconds gave terminal extensor relaxation, and no rebound phenomenon. But if it was compounded with the ipsilateral stimulus in its last 2 seconds, then on synchronous cessation of the two stimuli a flexor rebound contraction appeared. Is it perhaps possible that in this experiment (where augmentation of flexor rebound contraction occurs on synchronous cessation of the two stimuli) the flexor rebound is to be considered more a part of the contralateral reaction than of the ipsilateral; whereas in the other cases here described (where depression of flexor rebound occurs) the rebound is to be considered more as a part of the ipsilateral reaction? As a possible factor in the differences in the two cases it should be noticed that in the instance just described there was extensor terminal relaxation in the "pure" extension-reflex—as it were, a latent flexor rebound; whereas in the experiment described immediately before this one there was extensor after-discharge—which would be antagonistic to a flexor rebound in the ipsilateral flexion-reflex if the two were synchronously compounded.

In another experiment the ipsilateral flexion-reflex and the contralateral extension-reflex were both of "spinal" type, and neither was succeeded by a flexor rebound contraction on cessation of stimulation. When, however, the contralateral stimulus was applied late in the period of the flexion-reflex—and of sufficient strength to reduce completely the contraction of the flexor,—on synchronous cessation of the two stimuli there appeared a marked flexor rebound contraction. This commenced about 0·4 second after termination of double stimulation, and when it disappeared there was a slight extensor rebound contraction [see xvii. fig. 2].

### 3. Flexor Rebound Contraction after both Reflexes.

In a few experiments in which flexor rebound contraction occurred on cessation both of the ipsilateral stimulus and of the contralateral the two stimuli have been compounded and synchronously terminated.

In one such case there was a flexor rebound after an extension-reflex of 2 seconds' duration, and a larger flexor rebound after an ipsilateral flexion-reflex of the same duration. When the two were synchronously compounded for a period of 2 seconds there was an augmentation of the flexor rebound which became rhythmic in character—the rebound phenomenon consisting of three "complete" beats.

In another case (fig. 20), where, however, the contralateral reaction had previously been one of abnormal flexion, the "pure" reactions were followed by somewhat similar flexor rebounds. Here there was an augmented flexor rebound after double stimulation (again for 2 seconds). It was augmented as regards the flexor rebound after the flexion-reflex (and of course as regards that after the extension-reflex) in height, but not in the duration of the movement. Later in the experiment the flexor rebounds disappeared from the "pure" reactions, and no flexor rebound was

observed on synchronous termination of the two stimuli in a compound reaction.

In a third instance augmentation of the flexor rebound was also observed after double stimulation, but here the augmentation occurred more in the duration than in the extent of the reaction.

### B. Extensor Terminal Contraction Present.

In the decerebrate preparation the ipsilateral flexion reflex on cessation of the evoking stimulus may be succeeded by an extensor rebound contraction which may be maintained—so that it may appear similar to the tonic after-discharge of the extension-reflex. This may be modified after the termination of a synchronous application of two antagonistic stimuli. So too may be a "tonic" extensor after-discharge in the contralateral extension-reflex.

#### 1. Extensor After-Discharge in the Contralateral Extension-Reflex.

Where the ipsilateral flexion-reflex is not followed by an extensor rebound, and where the contralateral extension-reflex is followed by an extensor after-discharge of maintained contraction, the cessation of a double stimulation may be followed by an extensor rebound contraction even when during double stimulation there is a complete suppression of the extensor contraction. In one experiment in which this was seen the extension-reflex was followed by a state of diminishing maintained contraction. The flexion-reflex was of "spinal" type, and not followed by any rebound contraction. When the two antagonistic stimuli were applied and terminated synchronously there was complete absence of extensor contraction (there was flexor augmentation) during double stimulation, but 1 second after the synchronous termination of the two stimuli there commenced a well-marked extensor contraction. This slowly increased in extent, so that its maximum was attained about 2 seconds after its commencement, and then it began to diminish as slowly. In extent it was greater at its maximum than the after-discharge of the "pure" extension-reflex. In two succeeding reactions the ipsilateral flexion-producing stimulus was applied 1 and 2 seconds after the commencement of the extension-reflex. In both cases the period of double stimulation which then ensued was one of between 3 and 4 seconds. The extensor rebound contraction was progressively smaller, and at the same time the flexor after-discharge became of greater duration; that is to say, there was a greater interval of time between the cessation of double stimulation and the commencement of flexor relaxation. In the next recorded reaction the ipsilateral stimulus was first applied, and then after an interval of about 2·5 seconds the contralateral stimulus was commenced. The period of double stimulation then persisted for about 3 seconds, and conditioned an

augmentation of flexor contraction. There ensued an extensor rebound contraction on cessation of the two stimuli—and this was again smaller than before (for the last two reactions here described, see xv. fig. 9).

In another experiment there was again a well-marked tonic extensor after-discharge in the extension-reflex, but no extensor rebound in the flexion-reflex. Here it was found that when a contralateral stimulus was applied late in the period of a flexion-reflex, there was a well-marked extensor contraction during the period of double stimulation. On cessation of the double stimulation, there was at once a marked augmentation of this contraction. Its extent was nearly the same as that of the after-discharge of the "pure" extension-reflex evoked with the same strength of contralateral stimulation—as if here the presence of the ipsilateral stimulus held back the extensor from the attainment of the full extent of its contraction, and on cessation allowed the extensor to pass into the state of tonic after-discharge, just as though there had been no interference with the contralateral stimulus. Later in this experiment there was a very slight extensor rebound contraction after the ipsilateral flexion-reflex. The extension-reflex was then evoked, and late in the period of it an ipsilateral stimulus was applied. It was relatively much stronger than before. This produced complete abolition of extensor contraction, and at the same time the flexor contraction was slightly greater than in the "pure" flexion-reflex. On simultaneous cessation of the two stimuli the flexor relaxed slightly more slowly than in the "pure" flexion-reflex, and, about 0·5 second after cessation of the stimuli, there was a well-marked extensor rebound contraction. This was again of the appearance of a tonic after-discharge, but was not of so great an extent as in the "pure" extension-reflex (fig. 3; see also xvii. fig. 6).

In a third experiment of this nature there was again an extensor after-discharge of great extent and duration in the extension-reflex, but no rebound contraction in the flexion-reflex. The two stimuli were applied and terminated synchronously—the period of double stimulation being one of 2 seconds. With the strength of stimuli used the flexor contraction was almost completely abolished during double stimulation; at the same time the extensor contraction was greatly reduced. On cessation of the two stimuli the extensor contraction gave place to partial relaxation. This soon attained its greatest depth, and there persisted for about 1·5 seconds. It then became reëstablished, but its extent was not nearly as great as that of the extensor after-discharge in the "pure" extension-reflex.

### 2. Extensor Rebound Contraction in the Flexion-Reflex as well as Extensor After-discharge in the Contralateral Extension-Reflex.

It may occur that there is an extensor rebound contraction after the ipsilateral flexion-reflex as well as a tonic extensor after-discharge after

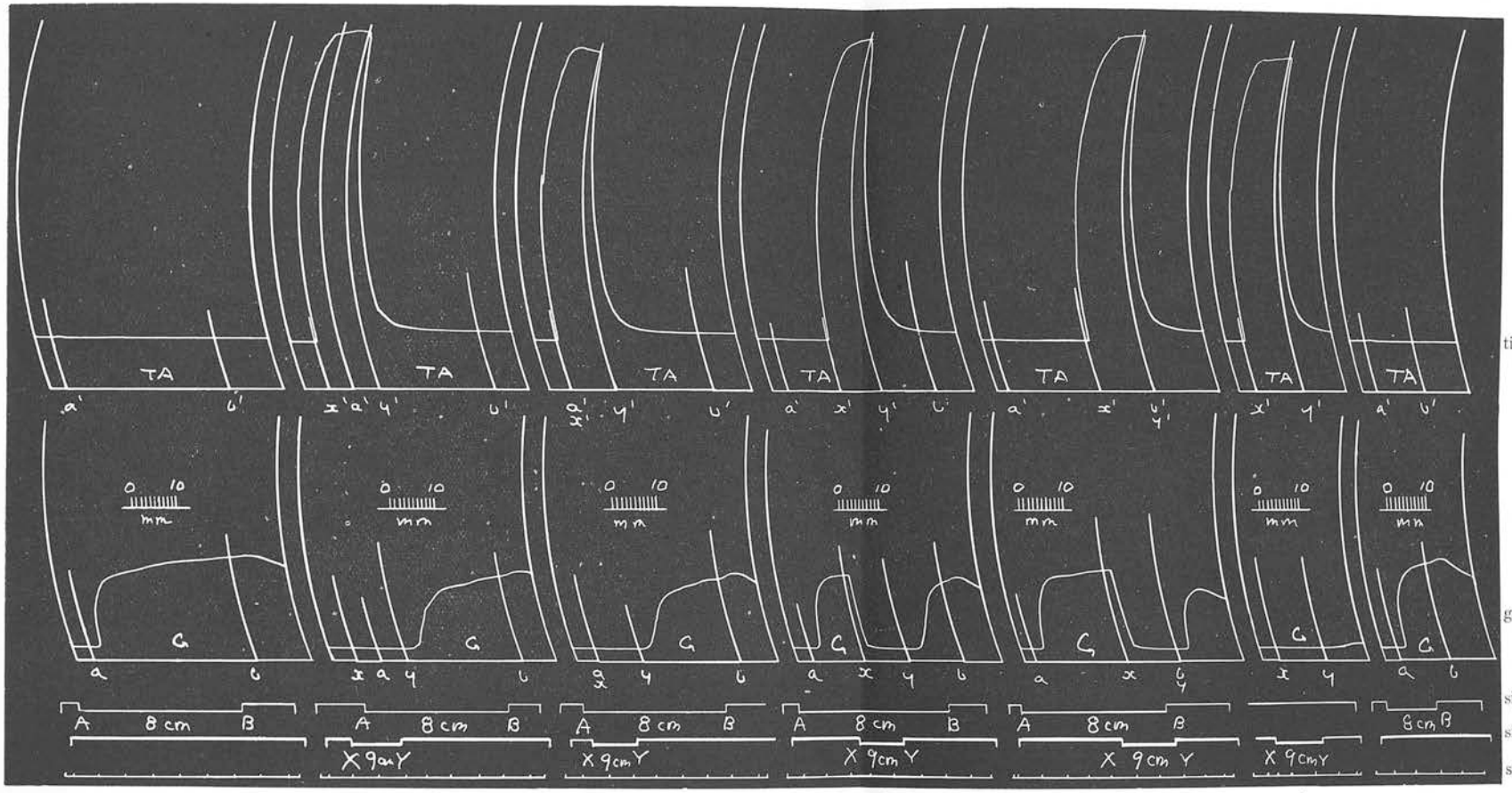


FIG. 3.—Experiment C, clxiv., record 262, 6197 ; 3/12/12.—Decerebrate cat. A series of reactions obtained 2 hours and 57 minutes after decerebration—minute intervals.

Reaction *a* is a "pure" extension-reflex, the duration of stimulation being the same as that of the contralateral "background" stimuli used in the following compound reactions.

Reaction *g* is another "pure" contralateral one, but of shorter duration. In *a* observe the tonic extensor after-discharge ; and in *g* note that there is indication of a slight "extensor rebound contraction after excitation."

Reaction *f* is a "pure" ipsilateral flexion-reflex taken with the same strength and duration of stimulus as that used in the compound reactions. On cessation of stimulation there is a very slight extensor rebound contraction.

Reactions *b*, *c*, *d*, and *e* are compound reactions in which the contralateral extension-reflex is the "background" and the ipsilateral interrupting stimulus is applied at different points in the period of the extension-reflex. In *b* the ipsilateral stimulus is first applied and first withdrawn.

In every case there is complete extensor suppression during double stimulation. In the third phases of the compound reactions ($y$, $y'$–$b$, $b'$) there is extensor restitution. Comparing *b*, *c*, and *d*, this appears to be a sharper movement and one of greater extent the later the ipsilateral stimulus falls. Note on withdrawal of the contralateral "background" stimulus there appears to be an indication of an "extensor rebound contraction after excitation." In *e* the two stimuli are synchronously withdrawn. Cessation of stimulation is followed by an extensor rebound contraction which is of less extent than the extensor after-discharge in the "pure" extension-reflex. In this series the flexor contraction during double stimulation appears to be slightly greater the later the ipsilateral stimulus falls in the period of the "background" extension-reflex ; and it seems to be greater than that in the "pure" flexion-reflex.

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the contralateral extension-reflex. Later in the first of the three experiments quoted above an extensor rebound appeared after the flexion-reflex (fig. 4). At this same period the contralateral extension-reflex had disappeared, but cessation of contralateral stimulation was followed by an extensor rebound contraction of comparatively short duration (about 2 seconds) and small extent. The extensor rebound after the flexion-reflex was of about the same extent but of long duration—more closely resembling an extensor tonic after-discharge. When the two stimuli were synchronously applied and terminated, the flexor contraction was delayed in onset but not reduced in extent. Cessation of the two stimuli was immediately followed by flexor relaxation and by a very large extensor rebound contraction. This was of about 3·5 times the extent of either of the rebound contractions in the "pure" reactions, but of a duration of about 0·75 second only. It was again followed by a second extensor rebound contraction which more nearly approached those of the "pure" reactions in appearance. In a series of reactions the two antagonistic stimuli were then synchronously applied and terminated, but the ipsilateral stimulus was progressively increased in strength. The extensor rebound contraction at this stage of the experiment was smaller than before, but progressively increased in extent with increase in the strength of the ipsilateral stimulus.

In another experiment the flexion-reflex was followed by a well-marked extensor rebound contraction of maintained type. The extension-reflex was followed by a well-marked tonic maintained extension. When the two stimuli were synchronously compounded and terminated, there was a diminution of the extent of flexor contraction and almost complete abolition of extensor contraction in the immediate compound phenomena. Cessation of the two stimuli was followed by an extensor rebound contraction. The fall of the flexor in relaxation was slightly more rapid than in the "pure" reaction. The extensor rebound was of rather greater extent than that either of the extensor rebound contraction in the flexion-reflex or of the extensor after-discharge in the extension-reflex. Having attained its maximum in about 0·4 second it, however, at once gave place to relaxation; and in about 1·3 seconds from the cessation of double stimulation the level of rest was attained—whereas the terminal phenomena of extensor contraction in both the "pure" flexion-reflex and the "pure" extension-reflex were maintained contractions of several seconds' duration. Immediately after this the double stimulation was again applied; but here the contralateral extension-reflex was allowed to run for about 4·5 seconds before the commencement of the ipsilateral stimulus. In the period of double stimulation there was not a complete relaxation of the extensor (the extension reaction was more vigorous than before). Cessation of the two stimuli was again followed by an extensor rebound contraction which was exactly similar to the previous one. It, however, appeared summated upon the level of extensor contraction which obtained

at the period of cessation of stimulation. As before, this immediately gave place to relaxation on reaching its maximum. But the extent of relaxation was not so complete as before, and there then ensued a state of maintained

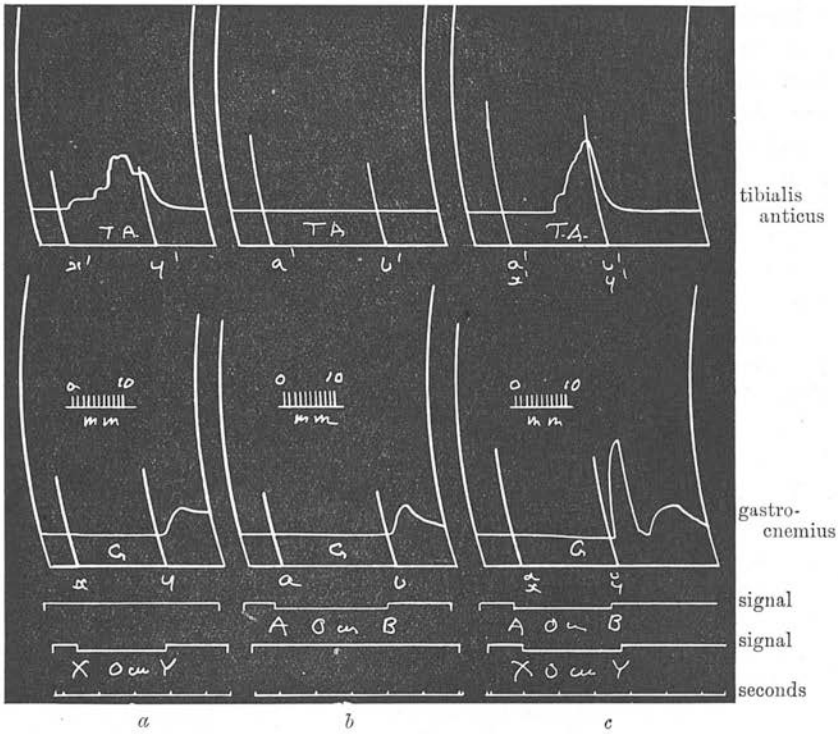


FIG. 4.—Experiment C, cxxvii., record 245, 5713; 7/11/12.—Decerebrate cat. Three reactions obtained 3 hours and 17 minutes after decerebration—minute intervals.

Reaction *a* is a "pure" flexion-reflex. Note the extensor rebound contraction of "maintained" form.

Reaction *b* is a "pure" contralateral one. There is no action during stimulation, but cessation of stimulation is followed by an extensor rebound contraction which is not maintained.

In reaction *c* the two reflexes are synchronously compounded. The flexor contraction during double stimulation is retarded in onset, but appears to be of greater extent than that in the "pure" flexion-reflex. On cessation of double stimulation there is flexor relaxation and a marked extensor rebound contraction. This is greater in extent than the sum of the extensor rebounds in the "pure" reflexes, but it is of short duration. It is followed by a more maintained extensor rebound phenomenon.

This record seems to demonstrate a case of augmentation of extensor terminal phenomena in the compound reaction. And this augmentation is greater than the sum of the two "pure" extensor rebound contractions.

contraction which resembled the tonic extensor after-discharge [see xv. fig. 7, reactions *b* and *c*.]

In a third experiment there was a badly maintained tonic extensor after-discharge in the contralateral extension-reflex and an extensor rebound of the maintained type in the ipsilateral flexion-reflex. The extensor contraction in the extension-reflex was of large extent; and both

the flexion-reflex (which was also of good extent) and the extension-reflex were of "spinal" type. The two stimuli were then synchronously applied and terminated. During the period of double stimulation there was algebraic summation—the contraction of each of the two antagonistic muscles being reduced in extent in comparison with the extents in the "pure" reactions. On cessation of double stimulation there was a very small and irregular extensor rebound contraction of very short duration. This at once gave place to a relaxation which brought the muscle below its level of rest. There it remained for about 1·5 seconds, and then again rose in a slight tonic contraction of long duration. Later in the same experiment, the period of double stimulation was commenced about 4 seconds after the commencement of the extension-reflex. Cessation of the two stimuli was followed by a small but regular extensor rebound contraction. This was of short duration—about 0·75 second—and gave place to a relaxation which brought the extensor to the level of rest (fig. 1).

In a fourth experiment the stimuli used were brief—of 1 second duration only. Here it was found that weak "pure" ipsilateral stimuli of this duration were followed on cessation of stimulation by a slight extensor rebound contraction. This was greater the weaker the stimulus was, and if the stimulus used was increased in strength in a series of reactions the extensor rebound gradually disappeared. This disappearance was not a general "fatigue" phenomenon, for a weak stimulus then repeated evoked again an extensor rebound. The "pure" extension-reflex—of the same duration of stimulation and of a strength unaltered throughout this part of the experiment—was followed by an extensor rebound contraction without preceding relaxation. When weak ipsilateral stimuli were compounded with this strength of contralateral stimulation, it was found that augmentation of flexor contraction occurred during double stimulation, and that there was complete relaxation of the extensor. Synchronous termination of the two compounded stimuli was followed by an extensor rebound greater than that of the extension-reflex—and of course much greater than that of the flexion-reflex. The difference between the level of contraction of the extensor in this rebound and in the rebound contraction of the extension-reflex was greater than the height of the extensor rebound contraction of the flexion-reflex. The extensor rebound contraction of the compound reaction was greater in extent the weaker the ipsilateral stimulus was (fig. 5). A series of compound reactions in which the value of the ipsilateral stimulus was gradually increased from a very weak strength to a very strong one was then taken (fig. 6). Again it was found that during double stimulation with weak ipsilateral stimuli there was augmentation of flexor contraction, and that the terminal extensor rebound contraction was greater than in the "pure" extension-reflex. But as the strength of the ipsilateral stimulus was gradually increased the extent of the extensor rebound contraction gradually diminished—until at last it was nearly abolished.

Weak ipsilateral stimuli of short duration seem to augment, and strong to depress, extensor terminal rebound contraction in compound reactions in which the stimuli are synchronously withdrawn. The fact that even after complete extensor relaxation during double stimulation there may occur an

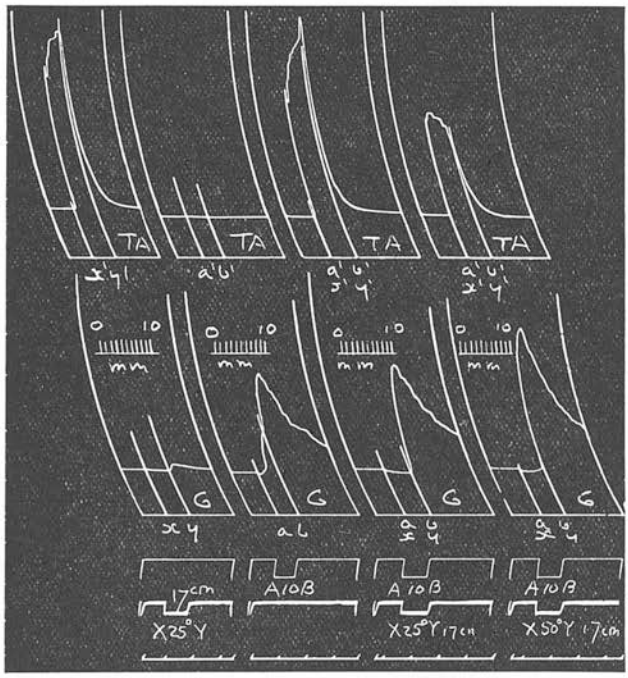


FIG. 5.—Experiment C, clxxiv., record 308, 8187; 11/3/13.—Decerebrate cat. Four reactions obtained 5 hours and 6 minutes after decerebration—minute intervals.

Reaction *a* is a "pure" flexion-reflex. There is a slight extensor rebound contraction. The strength of stimulus is very weak.

Reaction *b* is a "pure" extension-reflex. On cessation of stimulation there occurs a sudden augmentation of extensor contraction. This dies slowly after attaining its maximum.

In reaction *c* the stimuli used in *a* and *b* are synchronously compounded. Extensor relaxation occurs during double stimulation. On withdrawal of the two stimuli there occurs an extensor rebound somewhat similar to that in *b*, but of slightly greater extent.

In reaction *d* the ipsilateral stimulus is considerably weaker than that used in *a* and *c*. Cessation of the two compounded stimuli is followed by an extensor rebound similar to that in *b* and *c*. but considerably greater in extent. The contralateral stimulus here is of the same strength as that used in *b* and *c*, and in a "pure" ipsilateral reaction of the same value as that here compounded there was an extensor rebound rather greater than that in *a* (see reaction *e* of the following figure). The extensor rebound of this compound reaction is greater than the sum of those in the "pure" reactions compounded.

This figure therefore demonstrates summation and augmentation of the extensor rebounds when weak ipsilateral stimuli are used.

extensor rebound contraction greater than that in the "pure" flexion-reflex (for this see also fig. 14, reaction *e*) is of great interest, because it lends support to the view that there is a central process which underlies extensor after-discharge. In such cases there can be no peripheral self-generated extension-reflex such as that which in the ordinary extension-reflex might

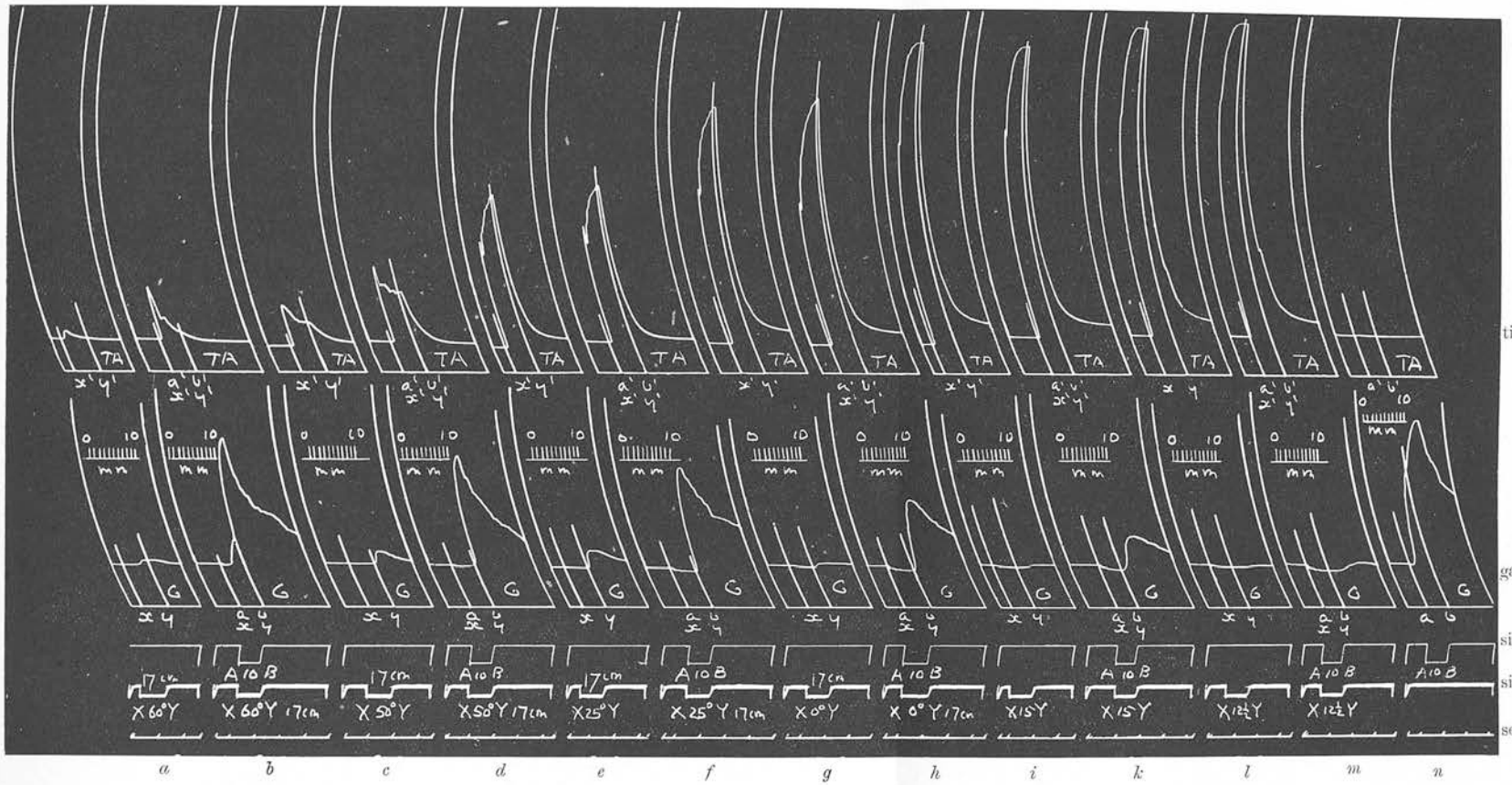


FIG. 6.—Experiment C, clxxiv., record 308, 8195 ; 11/3/13.—Decerebrate cat. A series of reactions obtained 5 hours and 12 minutes after decerebration—half-minute intervals.

Reaction *n* is a "pure" extension-reflex taken with the strength and duration of contralateral stimulation used in the compound reactions. Note the extensor after-discharge. This is larger than in a similar reaction obtained before the series was commenced (compare with reaction *b* in the preceding figure).

Reactions *a*, *c*, *e*, *g*, *i*, and *l* are "pure" ipsilateral flexion-reflexes obtained with progressively increased strengths of stimuli. Each stimulus is of the same value as that compounded in the immediately succeeding compound reaction. Observe that in this series of "pure" flexion-reflexes there is extensor rebound contraction. As the strength of stimulation is increased this at first increases, but then decreases until, in reaction *l*, it is almost absent.

Reactions *b*, *d*, *f*, *h*, *k*, and *m* are compound. The compounded stimuli are synchronously commenced and terminated. The contralateral stimulus is of constant strength throughout the series, but the strength of the ipsilateral stimulus is progressively increased. In each compound reaction the strength of ipsilateral stimulation is the same as that used in the immediately preceding "pure" ipsilateral reaction. In *b* there is an extensor rebound contraction which is greater than that in a preceding "pure" extension-reflex (not shewn)—although it is smaller than that in *n*. As the strength of the ipsilateral stimulus is increased in the compound reactions the extensor rebound gradually decreases, until in *m* it is almost absent. This is the case although there is about the same degree of extensor relaxation during double stimulation in all the compound reactions, and although there is a great extensor after-discharge in the final "pure" extension-reflex.

This series seems to demonstrate a summation of the "pure" terminal phenomena in the terminal phenomena of the compound reactions. It also seems to shew that here the absence of extensor rebound in the stronger "pure" ipsilateral reactions is due to an inhibitory suppression of it in the terminal phenomena.

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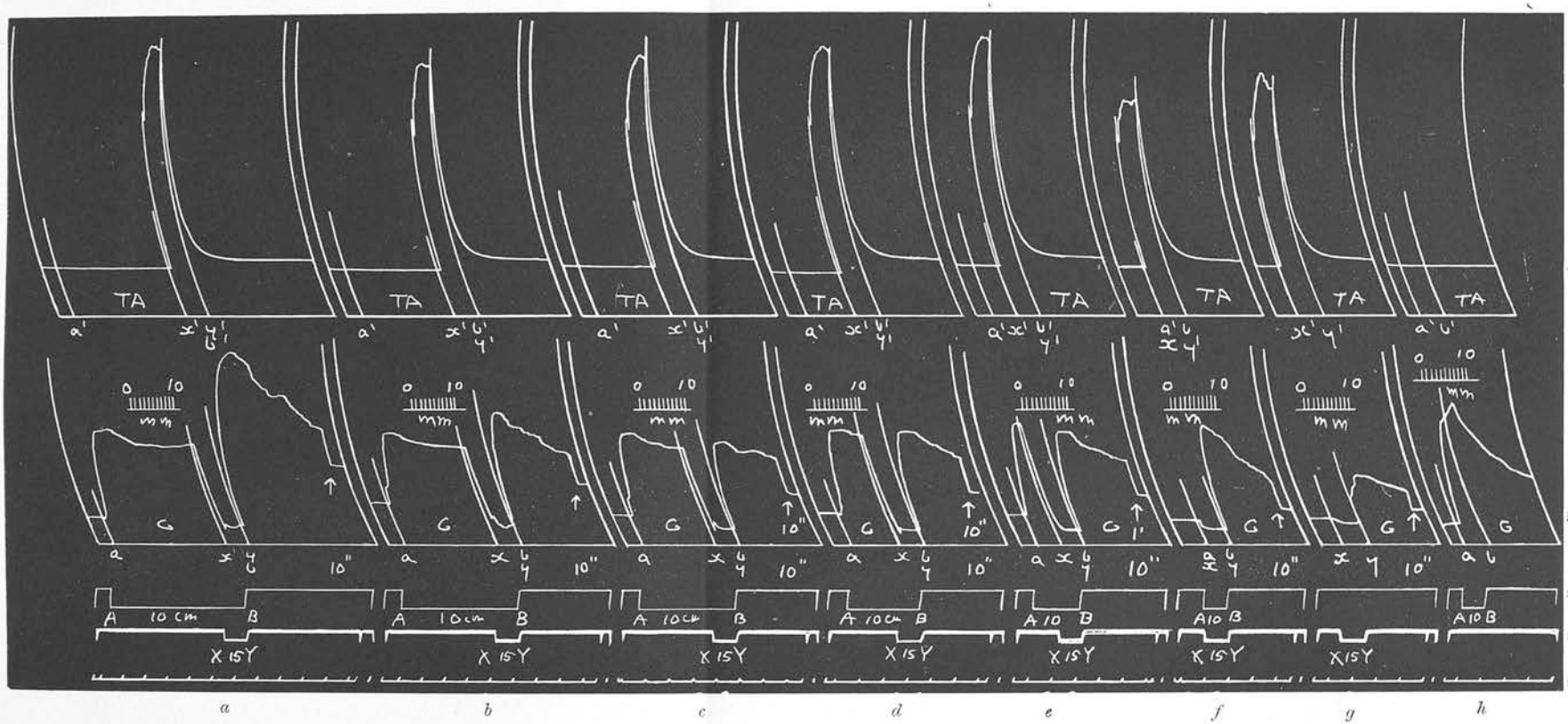


FIG. 7.—Experiment C, clxxiv., record 307, 8159 ; 11/3/13.—Decerebrate cat. A series of compound reactions obtained 3 hours and 27 minutes after decerebration—minute intervals. The reactions figured here immediately follow those reproduced in fig. 13—1 minute elapses between the last reaction of that figure and the first of this one.

[Reaction *f* of fig. 13 gives a "pure" contralateral extension-reflex of 6 seconds' duration—refer to it for comparison with reaction *a* here.]

Reaction *g* here is a "pure" ipsilateral flexion-reflex of the value and duration of stimulation used here throughout. It may be compared with reaction *g* of fig. 13 (taken just before the commencement of this series), with which it is very similar. Note the "extensor rebound contraction after inhibition."

Reaction *h* is a "pure" contralateral extension-reflex the duration of which is 1 second. Note the "extensor rebound contraction after excitation" and the following after-discharge. This is markedly less well sustained than in reflexes of greater duration. (Compare with reaction *f* of fig. 13, where the duration is 6 seconds.)

In reaction *a* the two stimuli are compounded for 1 second of double stimulation after the contralateral "background" has run for 5 seconds. On synchronous cessation of the two stimuli there is a marked extensor rebound contraction of a greater extent than the sum of the extents of extensor contraction in the after-discharge of the "pure" extension-reflex and the extensor rebound contraction of the "pure" flexion-reflex (*g*).

In reactions *b*, *c*, *d*, and *e* the duration of the preceding "background" stimulation is progressively reduced. As compared with the extent of extensor contraction which obtains at the commencement of double stimulation, it will be observed that the extent of the extensor rebound contraction progressively diminishes.

In reaction *f* the two stimuli are synchronously commenced and terminated. The extent of rebound contraction is greater than in *e*, but is less than that in *h*—a "pure" contralateral reaction of the same duration of stimulation.

In this instance (in which complete extensor relaxation occurs in every case during double stimulation) the extensor rebound contraction on synchronous cessation of the two stimuli appears to be greater the later the ipsilateral stimulus falls in the period of the contralateral.

carry on the reaction as "after-discharge." Here the augmented extensor rebound contraction is best looked upon as conditioned by the sum of the rebound of the flexion-reflex in the compound reaction and this central activity which tends to carry on the extension-reflex.

Earlier in this same experiment a "pure" contralateral stimulus applied for 6 seconds gave an extension-reflex which was followed by an extensor after-discharge. This was well maintained, and kept the level of extensor contraction at that which obtained during stimulation (fig. 7). Where the contralateral stimulus was applied for 1 second only there followed, on cessation of stimulation, an "extensor rebound contraction after excitation." In a series of compound reactions the contralateral stimulus was applied for different lengths of time (6, 5, 4, 3, and 2 seconds), and in every case during the last second of the period of contralateral stimulation an ipsilateral stimulus was added—the two stimuli then being synchronously withdrawn. In a final reaction the two stimuli were applied together and synchronously withdrawn after a duration of 1 second of double stimulation. The two stimuli were of constant value throughout the series. At the strength of ipsilateral stimulation used there was, in "pure" reactions, an extensor rebound contraction of maintained form but not of so great extent as the extensor after-discharge in the "pure" extension-reflex.

During double stimulation in the compound reactions there was, in every case, an extensor relaxation which brought the level of the extensor below that of "rest." Where the ipsilateral stimulus was first applied after the contralateral had run for 5 seconds there followed, on synchronous termination of the two stimuli, an extensor rebound contraction. This opened with a very rapid movement which, at its maximum, brought the level of extensor contraction far above that which obtained in the extensor rebound of the flexion-reflex or the extensor after-discharge of the extension-reflex. Its level was indeed greater than the sum of the levels of extensor contraction in these two phenomena. Having attained this maximum the extensor rebound slowly declined—but was still of greater extent than the extensor contraction during the "pure" extension-reflex 4 seconds after cessation of compound stimulation. Where the extension "background" preceded double stimulation by 4 seconds there was still an extensor rebound which was of greater extent than the extensor contraction of the "background"—but it was not of so great extent as the sum of the extensor contractions in the rebound of the flexion-reflex and the after-discharge of the extension-reflex. As the preceding "background" was shortened in duration, the extent of the extensor rebound on cessation of double stimulation fell, until it was actually below that of the contraction during the extension-reflex—that is, below that of the extension after-discharge. Repetition of a reaction in which the preceding "background" was again one of 5 seconds shewed the same phenomena as before; and a "pure" extension-reflex of 6 seconds' duration of stimulation again was followed by a well-maintained after-discharge, but by no extensor rebound from the

level of contraction during stimulation. It was noteworthy in this experiment that the extensor after-discharge of the "pure" extension-reflex seemed to be the better maintained the longer was the duration of contralateral stimulation.

### V. Successive Phenomena in Compound Stimulation: Stimuli of Asynchronous Termination — Contralateral Extension-Reflex ("Background") left in Action—No Rebound Contractions Present in the Simple Reflexes.

When the two antagonistic stimuli are applied together, and the ipsilateral stimulus is then withdrawn during the continued application of the contralateral extension-producing stimulus, there occur two phases in which the successive phenomena may be examined. For there is at first a phase in which the extension-reflex is in being, and in which the after-effects of the discontinued ipsilateral stimulus may be demonstrated in their alteration of the extension-reflex; and, secondly, there is a phase in which terminal phenomena may occur after the final withdrawal of the contralateral stimulus.

#### A. Successive Phenomena during the Continuation of the Contralateral Extension-Reflex ("Background") after Double Stimulation ["Third Phase" of the Compound Reaction].

When the contralateral extension-producing stimulus is first applied, and during its application an ipsilateral flexion-producing stimulus is applied and again withdrawn, there are four phases of the reflex phenomenon. In the first phase there is a state of "pure" contralateral extension; then there is the phase of double stimulation during which depression of the extensor contraction occurs and in which the flexor-contraction is not so great as that of the "pure" ipsilateral reaction; thirdly, there is the phase in which the contralateral extension-reflex again is uncomplicated by the immediate presence of the antagonistic stimulus; while, finally, there is the phase after the withdrawal of the contralateral stimulus, and in which the centres again return to the state of rest.

In the third phase—if there be no "rebound" phenomena after the cessation of the "pure" ipsilateral stimulus—two points arise for examination. These are the flexor after-discharge and the restitution of the state of uncomplicated extension. The restitution of extension may be affected by central states conditioned by the precurrent ipsilateral flexion-producing stimulus.

In general, it is found that the flexor after-discharge is reduced—when compared with that of the "pure" flexion-reflex. The latency of flexor relaxation is decreased—so that the flexor sooner commences to relax after the withdrawal of the ipsilateral stimulus; and the movement of relaxation

is a quicker one than in the "pure" reaction. This phenomenon is best seen when the "pure" flexion reaction is one distinctly of "spinal" type. Where the flexion after-discharge is well marked there may be a very distinct reduction of it in this third phase of the compounded reaction (fig. 3). On one occasion, however, there appeared to be an increase of the flexor after-discharge. Here at first the usual effect was seen, but later in the experiment there appeared a prolongation of the flexor contraction during the third phase of the reaction after the withdrawal of the ipsilateral stimulus. At first, immediately after that withdrawal, the flexor relaxed more quickly than in the "pure" reaction. But it did not fully relax, and—having reached a certain level of relaxation—it remained in partial contraction, which slowly decreased during the remainder of the period of contralateral stimulation. In this experiment the flexor often demonstrated a rapid tremor in the ipsilateral flexion-reflex. Still later in the experiment the cessation of the ipsilateral stimulus during the application of a contralateral was not followed at all by flexor relaxation. The flexor remained fully contracted, but demonstrated a rapid tremor during the period of the third phase of the compounded reaction. This was not present in the second phase (that of double stimulation), and the strength of contralateral stimulus used was at this stage in the experiment insufficient to give a reaction.

When attention is directed to the behaviour of the extensor muscle in this third phase of the compounded reaction it appears that in general it is characterised by a restitution of contraction. The actual height of contraction attained in this restitution—if the contralateral stimulus be continued, let us say, for 2 seconds after the cessation of the ipsilateral stimulus—often is as great as that which obtained in the first phase of the reaction when the contralateral stimulus had not yet been compounded with the ipsilateral. The height may even be greater. In other cases, however, the height of extensor contraction never attains again that of the "pure" reaction.

The curve of increasing contraction in this restitution differs from that of the initation of the "pure" extensor contraction in the extension-reflex. It is often rather irregular—whereas the curve of increasing contraction in the "pure" reaction is usually regular if that be of "spinal" type. It may, however, be regular in appearance. When that is the case its latency is greater, and the rise itself is a less rapid movement [see xv. fig. 7, reactions *a*, *e*, *f*]. Occasionally the latency of the commencement of this reconstitution after the cessation of the ipsilateral stimulus is less than that of the commencement of extensor contraction in the "pure" extension-reflex. This may occur when the latency of the "pure" reaction is comparatively great.

Series of compounded reactions were taken in these experiments—the time relations of the antagonistic stimuli being progressively altered, or their relative values progressively changed.

Where the time relations of the two stimuli have been altered in

successive reactions the strengths of the stimuli have been kept constant. It has been the rule to apply the contralateral stimulus for a period of 6 seconds, and to apply a 2-second ipsilateral stimulus at varying intervals of time after the commencement of the contralateral stimulus (for instance, 0, 1, 2, 3, and 4 seconds) (figs. 3, 8) [see also xv. fig. 7 (where, however, rebound phenomena are present)]. The restitution of extensor contraction after the cessation of the ipsilateral stimulus then usually appears to be greater the later in the period of contralateral stimulation the ipsilateral stimulus is applied. This is perhaps in line with the observation that the depression of extensor contraction during double stimulation is usually less the later the double stimulation is applied after the commencement of the contralateral stimulus. It is of interest that the restitution of extensor contraction in the third phase may be observed to be greater the later the ipsilateral stimulus is applied in the course of the "background," even in cases where the strength of the interrupting ipsilateral stimulus is so great that it produces complete extensor relaxation during double stimulation in every case (fig. 3). To test the amount of restitution of extensor contraction, a fixed period—say 1 second—after the termination of the ipsilateral stimulus may be selected, and the height of extensor contraction at that point in the reaction measured. When this is done it is found that the amount of contraction at this point increases the longer after the commencement of the contralateral extension-producing stimulus the ipsilateral stimulus is applied. It is at its smallest when the two stimuli are applied synchronously—the ipsilateral of course being then withdrawn during the continuation of the contralateral. At the same time the actual curve by which the extensor contraction is reconstituted appears as a sharper rise (equivalent to quicker contraction) the later the period of double stimulation occurs after the commencement of the contralateral stimulus. But it occasionally happens that the amount of reconstitution of extensor contraction, and the rapidity of the movement, are both greater when the period of double stimulation falls early than when it falls late.

Where the strengths of the two antagonistic stimuli have been altered in consecutive series of reactions their time relations have been kept constant—the contralateral stimulus usually being applied for a period of 6 seconds and the ipsilateral for one of 2 seconds, being applied 2 seconds after the commencement of the contralateral (fig. 9). In such cases it has been found that the height of extensor contraction after the cessation of double stimulation has more nearly approximated to the height before the commencement of double stimulation when the ipsilateral stimulus was relatively stronger than when it was relatively weaker than the ipsilateral —although the reverse of this has been observed. It has also been observed that the time within which the extensor attained its full degree of restitution of contraction after double stimulation has been shorter when the ipsilateral stimulus was stronger, even when there was no extensor rebound phenomenon in the "pure" ipsilateral flexion-reflex. Measured from the

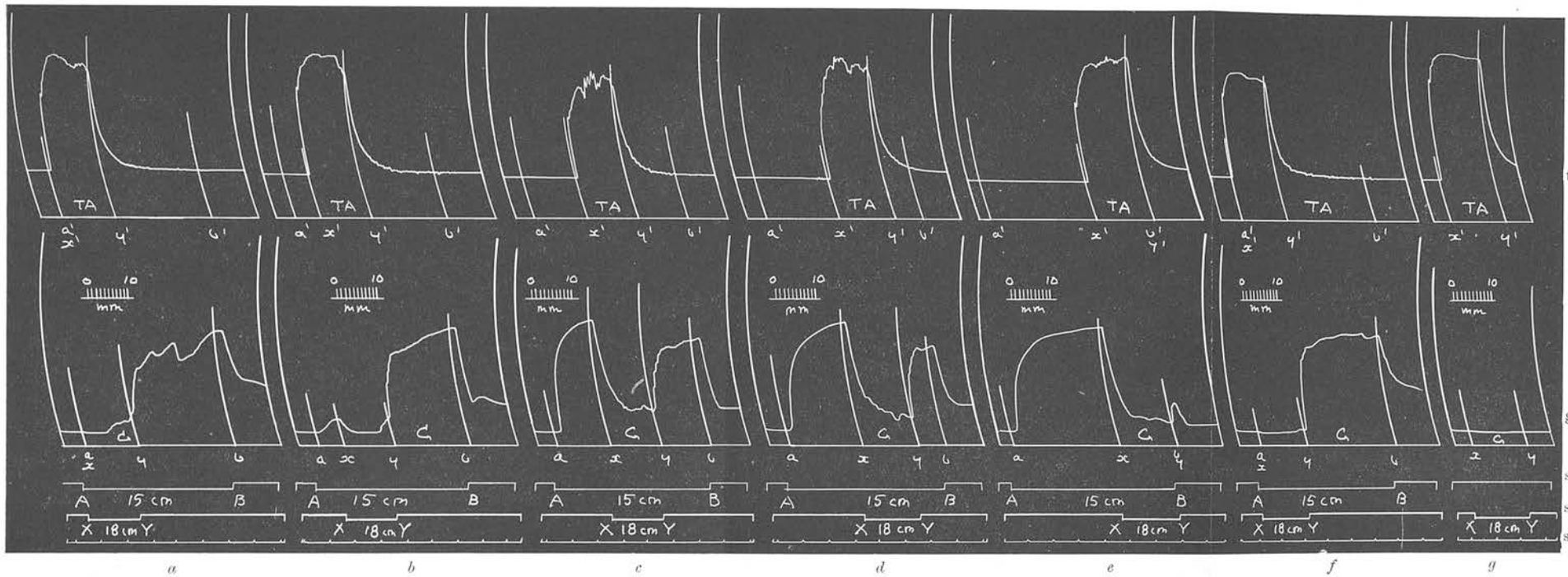


FIG. 8.—Experiment C, clxiii., record 261, 6135; 2/11/12.—Decerebrate cat. A series of compound reactions obtained 1 hour and 59 minutes after decerebration—minute intervals.

Reaction *g* is a "pure" ipsilateral one taken with the strength and duration of stimulation used in the compound reactions.

Reactions *a*, *b*, *c*, *d*, *e*, and *f* are compound. In them the same strength of ipsilateral and contralateral stimulus is used throughout, but the temporal relations of the two stimuli are varied. In *a* and *f* they are commenced synchronously. In *e* they are terminated synchronously, while in *b*, *c*, *d*, and *e* the ipsilateral stimulus is commenced about 1, 2, 3, and 4 seconds after the commencement of the "background."

Note that the extent of extensor contraction which persists during double stimulation seems upon the whole to be greater the later the ipsilateral stimulus falls. This is not absolutely the case, because in *d* and *e* it is smaller than in *c*.

If the extent of extensor contraction after 1 second duration of the "third phase" (ordinates $y$, $y'$–$b$, $b'$) be compared in the first four reactions, it will be found to be greater the later the ipsilateral stimulus falls—but again it is greater in *f* than in *a*.

In this series observe the extensor after-discharge in the "fourth" phases of the compound reactions. It will be found to be greater the earlier the ipsilateral stimulus falls. This applies as well for *a* as for *f*. In *e* note the slight extensor rebound contraction.

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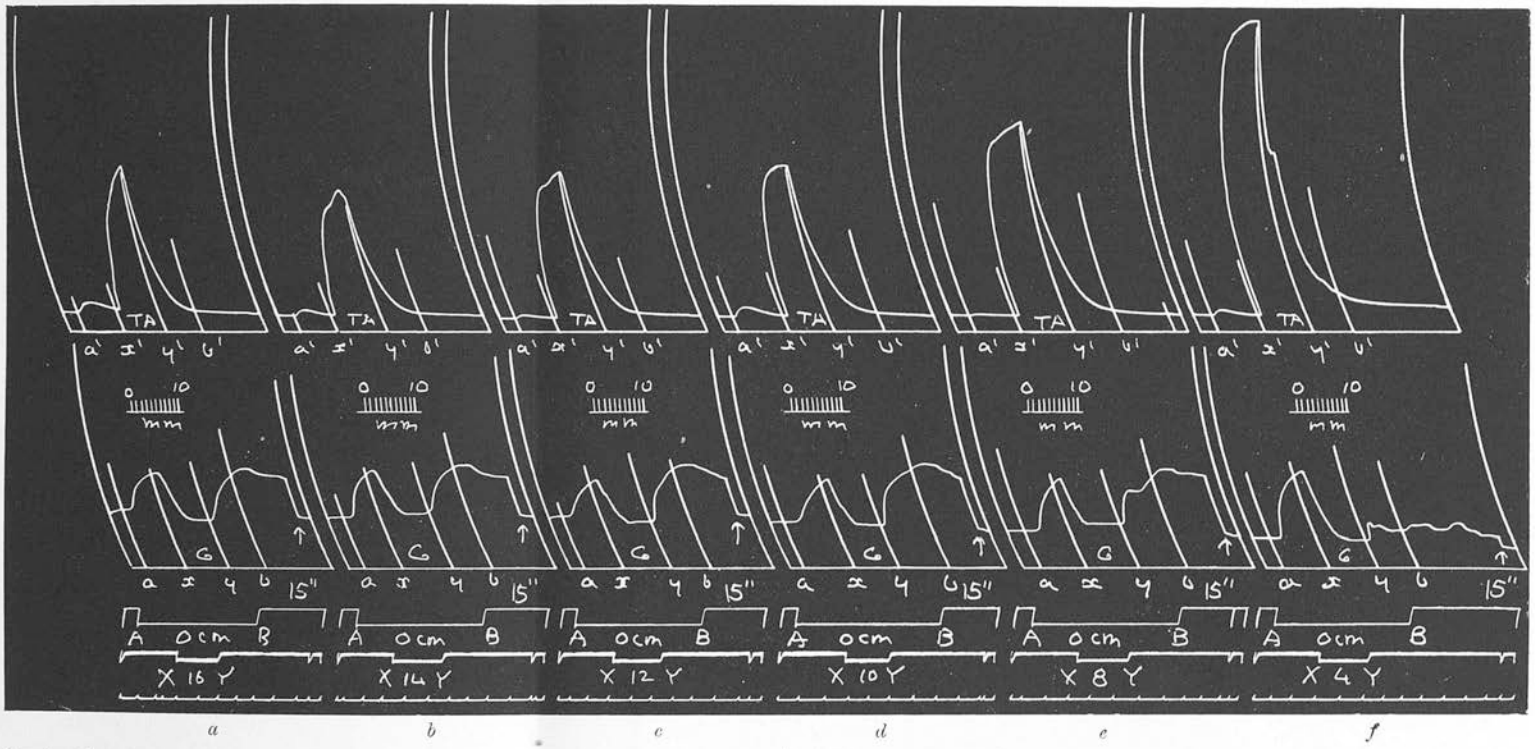


FIG. 9.—Experiment C, clxvi., record 295, 7497 ; 24/2/13.—Decerebrate cat. A series of compound reactions obtained 3 hours and 4 minutes after decerebration—minute intervals.

In this series the strength of the contralateral "background" is constant, but that of the interrupting ipsilateral stimulus is progressively increased. At the point marked in each reaction the drum was stopped for 15 seconds.

Throughout the series there is complete extensor relaxation during double stimulation. In the third phase the extensor restitution of contraction is progressively a sharper movement, and somewhat greater in extent, the stronger the ipsilateral stimulus up to reaction *d*. But in *e* it is again smaller, and in *f* almost completely suppressed. In this last reaction there is a greater flexor after-discharge than before, and it may be noted that in each "background" extension-reflex there is a slight preliminary phase of flexion.

Here, in the fourth phase, the extensor after-discharge appears to be increased up to reaction *e*, but in *f* is depressed along with the extensor contraction in the third phase.

GRAHAM BROWN, "Studies in the Physiology of the Nervous System."

level of extensor contraction during the period of double stimulation, the amount of restitution of extensor contraction has always been greater the stronger the ipsilateral stimulus. For the extensor in its restitution during the remaining phase of contralateral stimulation approximates to that level of contraction which would have obtained had the contralateral stimulus been uninterrupted by the ipsilateral, and the amount of extensor depression during double stimulation is greater the stronger the ipsilateral stimulus is.

In one experiment in which the strength of the interrupting ipsilateral stimulus was progressively increased it was observed that up to a certain point there was progressive increase in the extent of the extensor restitution of contraction in the third phase. But after this point was passed, and with strong ipsilateral stimuli, there was decrease of the extent of restitution until, with very strong stimuli, there was almost no restitution (fig. 9).

### B. Successive Phenomena after the Discontinuation of the Contralateral Extension-Reflex ["Fourth Phase" of the Compound Reaction].

On termination of the "pure" contralateral extension-reflex there often succeeds, in the decerebrate preparation, a state of tonic extensor after-discharge which may last many seconds, and carries the extensor muscle on in maintained contraction at that level of contraction which is exhibited at the period of cessation of the exciting stimulus. The question may arise here—how does a precurrent period of double stimulation, which precedes a short period of "pure" contralateral stimulation, affect this tonic after-discharge? We may limit ourselves to the consideration of these cases in which there is no similar terminal phenomenon of maintained extensor contraction in the ipsilateral flexion-reflex.

In a word, it may be said that as a rule there remains a maintained extensor contraction after the cessation of the contralateral extension-producing stimulus, and that this carries on the extensor contraction at the level attained in the restitution of contraction which occurs after the cessation of the period of double stimulation and when the contralateral stimulus is still in being. Instances in which the tonic extension was maintained even better than in the "pure" contralateral reflex (but that of shorter duration of contralateral stimulation) have occurred. More usually the tonic after-discharge carries on the muscle at the level present at cessation of stimulation (fig. 3). But cases in which the extensor after-discharge is markedly reduced also occur [see xv. fig. 3 (reactions *b*, *c*, *d*)]. This may take place when there is a well-marked extensor after-discharge in the "pure" extension-reflex, and it usually occurs as a sudden relaxation of the extensor contraction after cessation of stimulation. This relaxation may be "complete"—that is, may bring the level of contraction to the level of rest—or it may be partial. In either case it may be followed by

a partial augmentation of the extensor after-discharge. The relaxation is quite unlike the slow dying away of the normal tonic extensor after-discharge, as it occurs with great rapidity. In two of the series of such reactions (figs. 3, 8), in which the time relations of the two stimuli were progressively altered, it appeared that the depression of the tonic extensor after-discharge was greater the shorter was the interval of time between the cessation of the ipsilateral stimulus in the period of double stimulation and the cessation of the retained contralateral stimulus.

## VI. Successive Phenomena in Compound Stimulation: Stimuli of Asynchronous Termination—Contralateral Extension-Reflex ("Background") left in Action — Rebound Contractions present in the Simple Reflexes.

### A. Successive Phenomena during the Continuation of the Contralateral Extension-Reflex ("Background") after the Period of Double Stimulation ["Third Phase" of the Compound Reaction].

When a contralateral extension-producing stimulus is applied during a certain period of time and, within that period, compounded with an antagonistic ipsilateral flexion-producing stimulus (the second stimulus being applied after commencement of the first, and withdrawn before its termination), that which we may designate as the third phase of the resultant reaction extends in time from the moment of cessation of the ipsilateral stimulus (or of the period of double stimulation) to the moment of termination of the contralateral stimulus, which for a time is left in action.

This phase of the reaction is one of great interest. In it there tends to occur a reëstablishment of the "background" extension-reflex conditioned by the contralateral stimulus still in action. Under normal circumstances — examined in the previous section — the reëstablishment occurs as an activity conditioned by two antagonistic variable activities. Of these the one is the extension activity (extensor contraction and flexor relaxation) produced by the contralateral stimulus; the second is the normal flexor after-discharge. Each of these two activities is perhaps in its turn controlled by two antagonistic factors: in the case of the extension-reflex by antagonistic extension and flexion which vary relatively in value during the continuation of the stimulus and of which the factor of extension preponderates over that of flexion—$E > F$; in the case of the flexion after-discharge by antagonistic flexion (maintained flexor contraction, "inertia" of flexor centre?) and extension ("flexor rebound relaxation after contraction") which also vary relatively in value with duration of the period which elapses after cessation of stimulation and of which the factor of extension gradually preponderates over that of flexion—$E' > F'$. In either case the relative value of the factor of flexion as compared with that of

extension seems to be greater earlier in the period and less later in the period. It must be remembered, however, that in the extension-reflex the factor of flexion—when present at all – seems to be most pronounced in the earliest parts of the period of stimulation. Flexor contraction accompanied by extensor relaxation, or extensor relaxation alone, occurs usually in the first second of time, or the first and second seconds of time in the period of contralateral stimulation.[1] At the commencement of this third phase of the compounded reaction the contralateral stimulus is in full flood, and it is at any rate possible that this phenomenon of flexion activity in the extension-reflex may not again occur, or that it may be greatly depressed.

Upon the whole, it is perhaps most simple to regard the phenomena in the third phase of such a compounded reaction as somewhat equivalent to those which are conditioned when an extension-reflex is augmented by an increase in the strength of the contralateral stimulus which evokes it, but complicated by the presence of flexion after-discharge. During the second phase of the compounded reaction (or the phase of double stimulation) the extensor is in a state of contraction more or less equivalent to that which is conditioned by a comparatively weak "pure" contralateral stimulus. Immediately after this phase the extensor contraction augments —as it would do if the weak contralateral stimulus were suitably augmented. But at the same time there is present in the centres the activity of flexion after-discharge, and all that the terminal phenomena of the flexion-reflex imply. Here there is an ever-decreasing flexion activity. But immediately after the cessation of the ipsilateral stimulus this may be sufficiently strong to delay the onset of extension—that is to say, to make that onset a more gradual process than it would be if it were due merely to the augmentation of a "pure" contralateral extension-reflex. The different results obtained in these simple cases may be explained as due to variation in the relative values of the different factors. For instance, the flexion after-discharge may be relatively great. In such a case the restitution of extension in the third phase will be slow of attainment. If the flexion after-discharge be relatively small, the restitution of extension may be fast and great. That it may even in some cases be of greater extent than in the "pure" reaction may be explained as due to a relatively high value of the extension activity which may be supposed to cut short the flexion after-discharge of the "pure" reaction—even where that value is not sufficiently great to produce an extensor rebound contraction in the ipsilateral flexion-reflex.

But where rebound phenomena are present in the ipsilateral flexion-reflex it will be seen that the course of this third phase of the compounded reaction may be still further complicated.

The rebound phenomena of the flexion-reflex in the decerebrate preparation may be classed as of two chief forms.[2] In the first place,

[1] Paper XI. of this series—this Journal, vol. v., No. 3, p. 237, 1912.
[2] Paper IX. of this series—this Journal, vol. iv., No. 4, p. 331, 1911.

there is the comparatively rare "flexor rebound contraction after excitation." Here the level of contraction of the flexor is augmented after the cessation of the exciting stimulus. Allied to this (and probably its reciprocal) is the very rare phenomenon[1] of "extensor rebound relaxation after inhibition." This may be the reciprocal of the flexor contraction; but in the cases of flexor rebound contraction it has always been absent—probably masked by the absence of a sufficient degree of extensor tonus,—while in the instance in which it has been most clearly present there was no flexor rebound contraction. In the second form of flexion-reflex terminal phenomena is the common "extensor rebound contraction after inhibition." This is so often present that it must be regarded as the usual terminal phenomenon. In the "decerebrate" type of flexion-reflex this most commonly has the form of a comparatively slowly increasing extensor contraction which, when it has reached its maximum, is tonically maintained for many seconds. In de-afferented preparations this is not present. The extensor rebound then appears as a contraction phase immediately succeeded by a phase of relaxation. The reciprocal of this rebound contraction may be taken to be the ordinary relaxation of the flexor muscle at the end of the period of ipsilateral stimulation.

After the termination of an ipsilateral stimulus there appears to ensue either a state in which the flexion activity of the linked half-centres is increased, or one in which the extension activity of these half-centres is increased. The former state, when it occurs, seems to be usually of short duration—and then appears to pass over into the second. The second state, on the other hand, is a more lasting one. It is possible that either may complicate the phenomena in the third phase of such forms of compounded reactions as we are examining.

### 1. In Cases in which "Flexor Rebound Contraction after Excitation" is present in the Flexion-Reflex.

We may look, in the first place, at those instances in which the flexion augmentation occurs as a primary factor in the terminal phenomena.

In such cases, especially where the flexor rebound contraction is of comparatively long duration, it is by no means uncommon for there to appear a rhythmic phenomenon in the third phase of the compounded reaction. The flexor muscle—in place of the sustained rebound contraction—then exhibits a series of "beats" which more or less closely resemble the "beats" of that muscle in progression records. Reciprocal relaxations then occur in the contraction curve of the extensor muscle. This phenomenon may be present even when there is, at the time, no evident flexor rebound contraction. It is intended in a later paper more closely to analyse these rhythmic phenomena in compounded reflexes.

Where no rhythmic phenomena occur there is usually a retardation of

[1] Paper X. of this series—this Journal, vol. v., No. 3, p. 233, 1912.

the normal course of extensor restitution of contraction in the third phase of the compounded reaction. In one experiment in which this occurred there was, in the period of double stimulation, at first a marked relaxation of the extensor. As the period of double stimulation continued there appeared a slight and gradual restitution of extensor contraction—as in the flexion-reflex of "decerebrate" form. Immediately after the termination of the ipsilateral stimulus, and when the contralateral was then running alone, there appeared a relaxation of the extensor, which then gradually gave place to the usual restitution of extensor contraction. In this case there appeared, therefore, to be distinct evidence of a state of "extensor rebound relaxation after inhibition" in the flexion-reflex. Later in this experiment the same phenomenon was again observed. Here there was an accompanying flexor rebound contraction which, however, was not so great as in the "pure" flexion-reflex. Thereafter, and while the contralateral stimulus was still in action, the extensor restitution of contraction occurred; but the maximum level attained was not so great as that which would have obtained had the contralateral stimulus been uninterrupted by an ipsilateral [see xv. fig. 3, reactions *b* and *c*]. In another instance in which there was a flexor rebound contraction the extensor used was not the usual gastrocnemius-soleus (which I have, for convenience, generally termed simply "gastrocnemius"), but its isolated soleus component. Here during the period of double stimulation there was a certain (but slight) amount of restitution of extensor contraction. Immediately after cessation of the ipsilateral stimulus this was again reduced, so that the level of extensor contraction in the third phase was actually lower than in the phase of double stimulation [see xv. fig. 13, reaction *a*]. The extensor curve was here again rhythmic, and later in the third phase the normal restitution occurred with a very long latency.

In another experiment the ipsilateral stimulus when applied "pure" and of a certain strength was not followed by flexor rebound—but a stronger one of longer duration was. In this case the temporal relations of the antagonistic stimuli were varied. When double stimulation fell early in the course of the "background" reaction there was a certain amount of increasing extensor contraction late in the period of double stimulation. On withdrawal of the ipsilateral stimulus there was a well-marked flexor rebound contraction while the contralateral "background" stimulus was still in action. This was accompanied by a marked reciprocal extensor relaxation. During the course of the third phase of the compound reaction this again gave place to a complete restitution of extensor contraction, and on withdrawal of the contralateral stimulus the extensor remained in "tonic" maintained contraction—as in the "pure" contralateral extension-reflex. When double stimulation was made to fall later in the period of contralateral stimulation there was a smaller (or less maintained) extensor relaxation during the early part of double stimulation. Towards the end of that period there was greater restitution of extensor contraction,

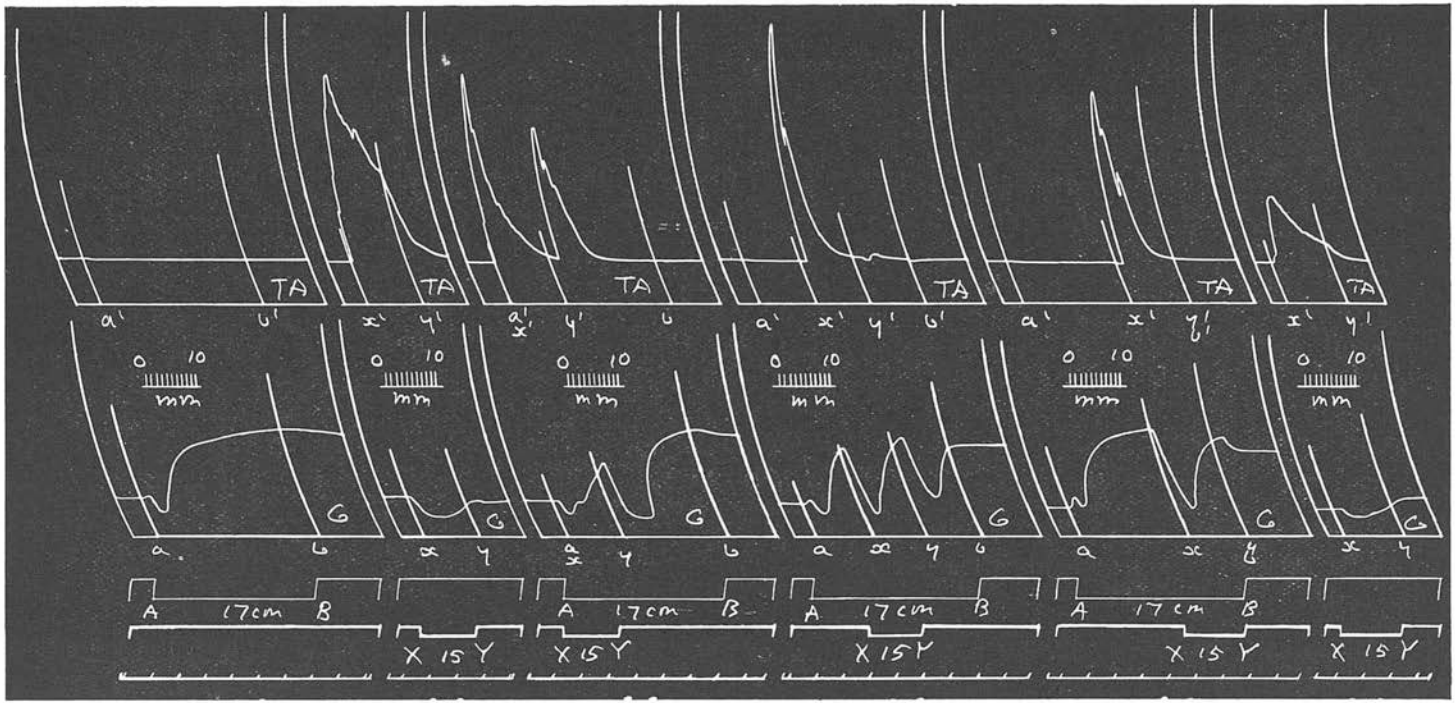


FIG. 10.—Experiment C, clxviii., record 298, 7666; 27/2/13. —Decerebrate cat. A series of compound reactions obtained 3 hours and 17 minutes after decerebration—minute intervals.

Reaction *a* is a "pure" extension-reflex of the strength and duration of excitation used in the subsequent compound reactions. Note the "decerebrate" type, and the extensor after-discharge.

Reactions *b* and *f* are "pure" flexion-reflexes evoked by stimuli of the same strength and duration as those used in the compound reactions. Note the absence of flexor rebound contraction (which was, however, present with stronger stimuli of greater duration). Note also the deterioration of this ipsilateral stimulus in value.

Reactions *c*, *d*, and *e* are compound in which the temporal relations of the two stimuli are varied.

Extensor restitution occurs during double stimulation and is greater the later the ipsilateral stimulus falls.

At the commencement of the third phase (ordinates *y*, *y'–b*, *b'*) there is extensor relaxation. This is greater and of longer duration the earlier the ipsilateral stimulus falls. It is reciprocally accompanied in *c* by a good flexor contraction, in *d* by a slight flexor contraction, but in *e* by no flexor contraction. The extensor relaxation is followed by reconstitution of contraction still during the third phase. This is followed, in the fourth phase, by extensor after-discharge—which appears to be smaller in extent the later the ipsilateral stimulus falls in the period of the "background."

still during double stimulation. On withdrawal of the ipsilateral stimulus there was a very slight flexor rebound contraction and a reciprocal extensor relaxation which was of less extent and duration than before. The "relative latency" of these phenomena (that is, the latency from the point of withdrawal of the ipsilateral "interrupting" stimulus) was greater than before. On withdrawal of the contralateral "background" stimulus there was again a "tonic" extensor after-discharge—restitution of extensor contraction having followed the relaxation phenomenon in the third phase. In a third reaction double stimulation was made to fall still later in the period of contralateral stimulation, and at the end both stimuli were synchronously withdrawn. Here, on withdrawal of the stimuli, there was no flexor rebound contraction, and only a slight relaxation of the extensor contraction—which had been reconstituted towards the end of the period of double stimulation. Thereafter the extensor remained in "tonic" maintained contraction. In this experiment the contralateral extension-reflex was markedly diphasic ("decerebrate" type), although there was no factor of evident flexor contraction (fig. 10).

### 2. In Cases in which "Extensor Rebound Contraction after Inhibition" is present in Flexion-Reflex.

In the second place we may examine those cases in which extensor contraction occurs as a primary factor in the terminal reflex phenomena of the ipsilateral flexion-reflex.

Even in these circumstances it occasionally happens that there is a depression of the extensor restitution in the third phase of the reaction after the cessation of the ipsilateral stimulus—that is to say, that occasionally the extensor does not return to the level of contraction which it would have had had there not been interference by an ipsilateral stimulus (figs. 11, 12, 13, also fig. 3) [see also xv., fig. 7, reactions *d*, *e*, *f*, *g*]. This has been observed to occur in an instance in which there was a rhythmic phenomenon during the phase of double stimulation—and here the restitution of extension in the third phase was broken by a rhythmic relaxation of the muscle (fig. 11). In another instance the strength of ipsilateral stimulation was comparatively great—so that there was a complete relaxation of the extensor in the phase of double stimulation. The extensor rebound contraction after the "pure" flexion-reflex was here very slight. The restitution of extension in the third phase was not complete, but it the more nearly approached completeness the later in the period of contralateral stimulation the ipsilateral stimulus was applied (fig. 3). In a third instance the restitution of extension in the third phase nearly approached the level which would have obtained had the contralateral stimulus been uncomplicated by the ipsilateral. In this case the restitution appeared to be a sharper movement the earlier in the period of contralateral stimulation the ipsilateral stimulus was applied [see xv., fig. 7].

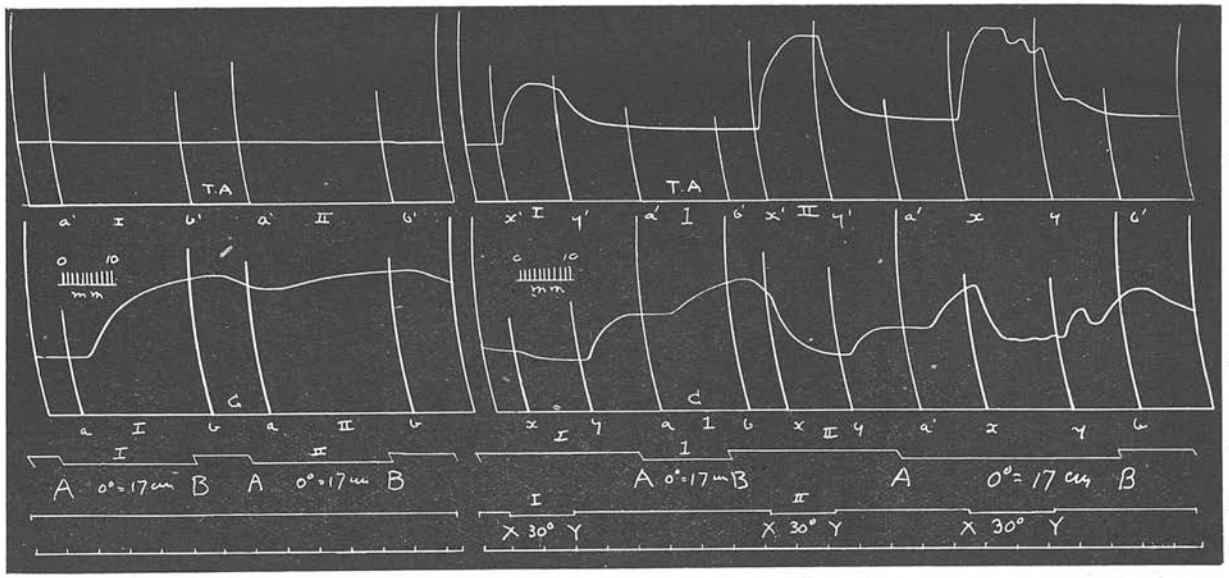


FIG. 11.—Experiment C, xxv., record 46, 1123; 15/3/11.—Decerebrate cat. Two reactions obtained 6 hours and 32 minutes after decerebration—2-minute interval.

In reaction *a* two "pure" contralateral stimuli are arranged in temporal succession with an interval 1·75 seconds between the termination of the first and the commencement of the second. The second stimulus causes an augmentation of the extensor after-discharge to a slightly higher level of contraction than that which obtains at the end of the first reaction.

In reaction *b* a "pure" ipsilateral flexion-reflex ("I") is first applied; then a "pure" contralateral extension-reflex; then a second flexion-reflex ("II"); then the two stimuli are compounded with an extension "background."

In the case of the first flexion-reflex ("I") there is a good inhibitory relaxation of the extensor. Cessation of stimulation is followed by an "extensor rebound contraction after inhibition" which is of maintained type. While this is in being the contralateral stimulus is added and causes a summation of extensor contraction on the extensor rebound. This summation at the end of 2·75 seconds of contralateral stimulation brings the level of extensor contraction slightly higher than that which obtains at the end of 2·75 seconds of stimulation in the first reflex of reaction *a*. About 1·2 seconds after the withdrawal of the contralateral stimulus the second flexion-reflex is applied. Relaxation of the extensor after-discharge is conditioned and the flexor contraction is greater than in "I." On termination of flexion-reflex "II" there is an extensor rebound contraction which is smaller than is that in "I."

While this is in being a second contralateral stimulus is again given. This is interrupted by a third ipsilateral stimulus. During double stimulation the phenomena are incompletely rhythmic—very slight and reciprocal augmentations and depressions of contraction in the two antagonists.

In the third phase (ordinates *y*, *y'-b*, *b'*) the phenomena are of great interest. There is not summation of the two positive factors—the extension of the extension-reflex and the extensor rebound of the flexion-reflex. Extensor restitution is broken by a relaxation present in neither. This is accompanied by a slight reciprocal augmentation of the flexor after-discharge. Thereafter extensor restitution again occurs.

This record seems to demonstrate a concealed factor of flexion in the early part of the terminal phenomena after the flexion-reflex, and its activation when that reflex is compounded against an extension "background."

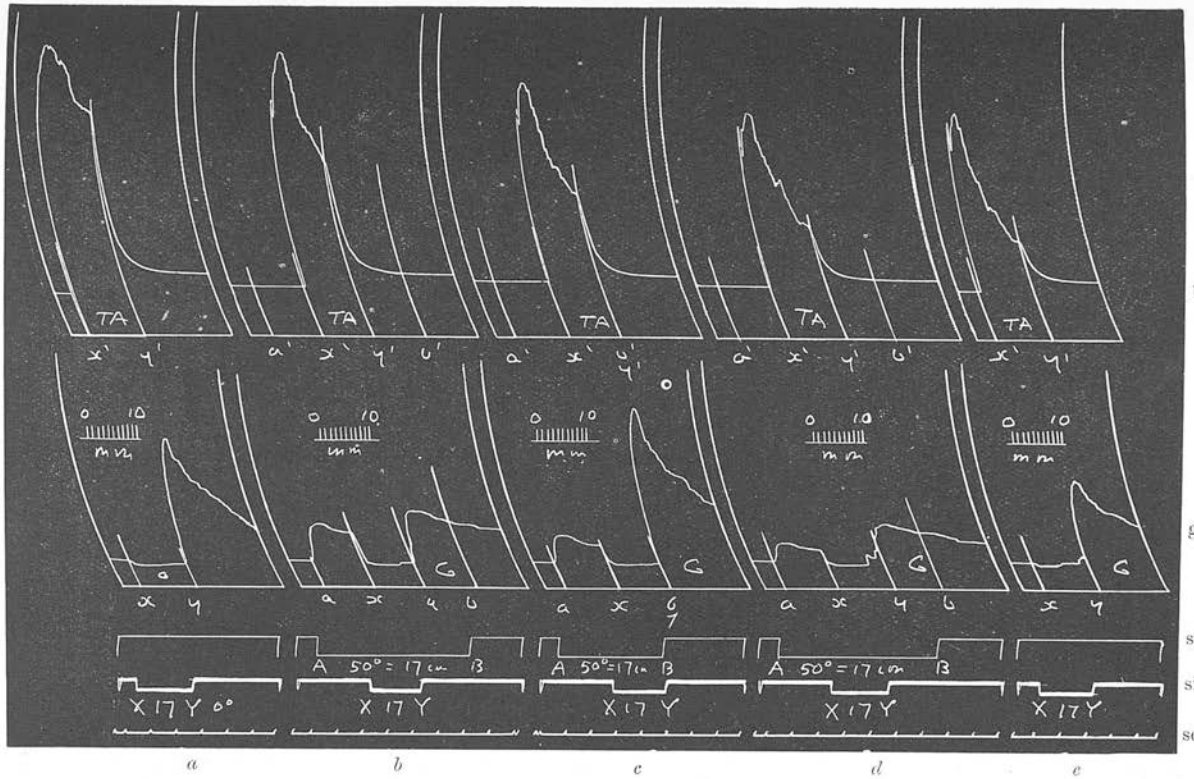


FIG. 12.—Experiment C, clxxiv., record 307, 8139; 11/3/13.—Decerebrate cat. A series of compound reactions obtained 3 hours and 6 minutes before decerebration—minute intervals.

Reaction *a* is a "pure" flexion-reflex of the strength and duration of stimulus used throughout. Note the large "extensor rebound contraction after inhibition."

Reaction *e* is a similar one taken at the end of the series. Note the deterioration of the extensor rebound, as well as that of the flexor contraction during stimulation.

The "pure" contralateral reactions of the strength and durations of stimulation here used gave during stimulation a level extensor contraction, and after stimulation a maintained after-discharge of the same level of contraction.

In reaction *b* the two stimuli are compounded. Complete extensor relaxation occurs during double stimulation. On withdrawal of the ipsilateral stimulus there is extensor restitution, and this carries the level of extensor contraction rather higher than that which obtains in the "pure" extension-reflex, but not nearly to the same height as that of the extensor contraction in the rebound phenomenon of the flexion-reflex.

In reaction *d* the same stimuli are arranged in the same manner and with the same results.

In reaction *c* the two stimuli are synchronously withdrawn at the end of the period of double stimulation. There then follows an extensor rebound phenomenon which is of greater extent than that in either of the "pure" flexion-reflexes here figured.

A possible explanation of the phenomena illustrated by this figure is that in this case there was a factor of flexion (or of extension depression) in the contralateral extension-reflex, and that this served partially to suppress the extensor rebound which otherwise might have been expected to summate upon the extension of the extension-reflex in the third phase of the compound reactions.

In one very interesting experiment (figs. 12, 13) in the "pure" flexion-reflex there was a very marked extensor rebound of peculiar type. In the third phase of a reaction in which this was compounded against an extension "background" there was extensor restitution of contraction. This was to a greater level of contraction than in the "pure" extension-reflex, but not nearly to the level of extensor contraction which obtained in the extensor rebound of the "pure" flexion-reflex. If the two stimuli were synchronously terminated there ensued a rebound contraction which was considerably greater than that in the "pure" flexion-reflex. It looks here as if during the being of a contralateral stimulus—although that evoked extension—there was a factor which was antagonistic to the extensor rebound of the flexion-reflex. Later in this experiment the temporal relations of the two stimuli were changed in a series of compound reactions. On cessation of double stimulation restitution of extensor contraction occurred—but in this case it did not bring the level of extensor contraction up to that which obtained in the "pure" extension-reflex. The restitution was a more rapid movement, and of greater extent, the later double stimulation fell in the period of the "background" extension-reflex. It was remarkable that when that double stimulation fell late, and there remained thereafter only 1 second duration of contralateral stimulation, a further augmentation of extensor contraction occurred on withdrawal of the contralateral stimulus.

But, when this phenomenon is present, the most usual occurrence in the third phase is an augmentation of extensor contraction; so that it is greater in extent than would have been the extensor contraction had the contralateral stimulus been uncomplicated. In fact, here summation of the extensor contraction of the contralateral stimulus and of the extensor contraction of the rebound phenomenon of the ipsilateral stimulus appears to occur [see xv. figs. 15, reaction *c*, 21, and 22]. If a just liminal contralateral stimulus is applied and compounded with an effective ipsilateral stimulus, there may appear an extensor contraction in the third phase of the compounded reaction which is greater than the extensor rebound of the ipsilateral reflex in extent. In instances in which the contralateral stimulus is effective, the third phase of the reaction is characterised by a restitution of extensor contraction after its inhibitory relaxation. The curve of restitution may be a sharper movement than the curve of the establishment of extension at the commencement of a "pure" contralateral extension-reflex. The level of contraction attained in the third phase is greater than that which would occur in a "pure" contralateral reaction after the same duration of stimulation. In series of reactions in which the time relations of the two stimuli are kept unchanged, but in which the strength of the ipsilateral stimulus is progressively increased, the level of extensor contraction in the third phase may be progressively heightened. This phenomenon seems to be related to the increase in the extent of extensor rebound which sometimes occurs when

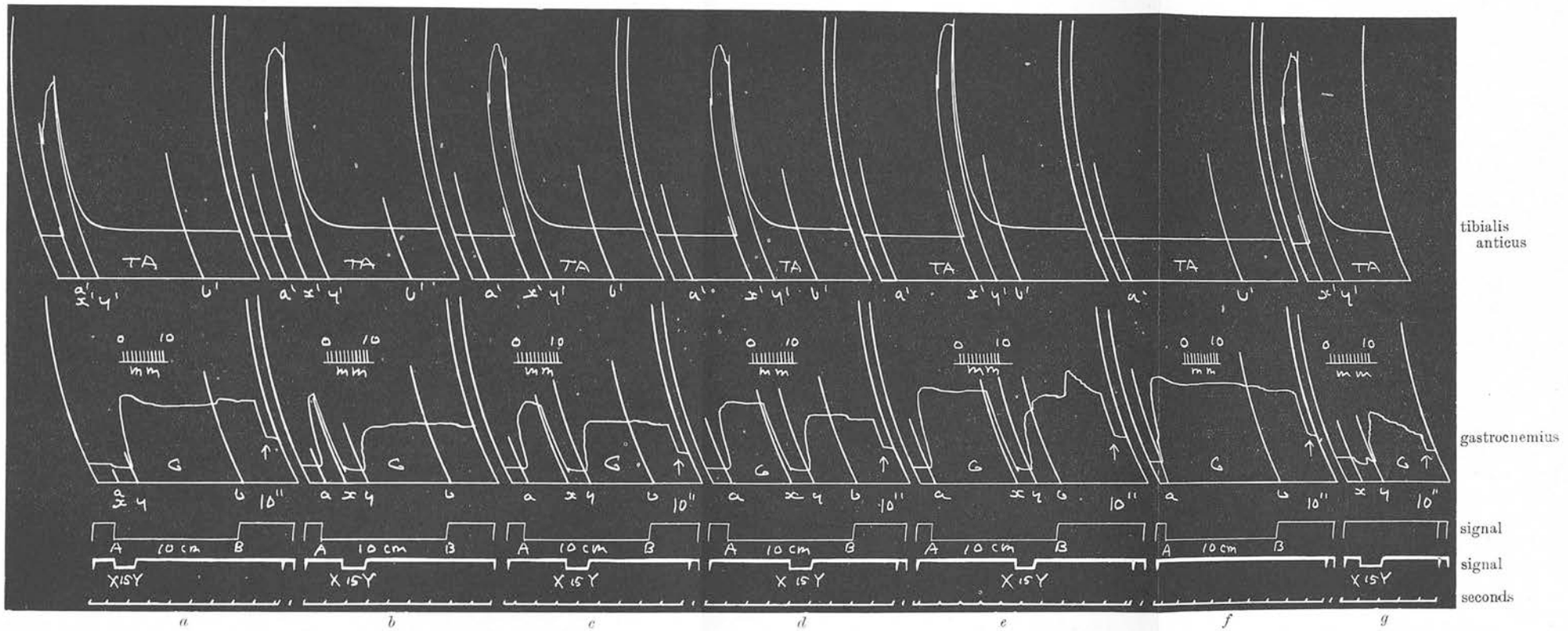


FIG. 13.—Experiment C, clxxiv., record 307, 8152; 11/3/18.—Decerebrate cat. A series of compound reactions obtained 3 hours and 20 minutes after decerebration—minute intervals.

Reaction *f* is a "pure" extension-reflex taken with the strength and duration of contralateral stimulation used in the preceding compound reactions.

Reaction *g* is a "pure" flexion-reflex taken under the same conditions.

In reaction *a–e* the two stimuli are compounded in different temporal arrangements—the ipsilateral stimulus being applied ever later in the period of the contralateral.

In *a*—double stimulation at the commencement of the period of the "background" extension—there is a sharp extensor restitution after double stimulation. In *b* this is very much less, but thereafter gradually increases the later the ipsilateral stimulus is applied.

Note that in no case is there summation of the extensor rebound of the "pure" flexion-reflex on the extensor contraction of the extension-reflex in the third phases of the compound reactions. In all the compound reactions the maximum of extensor contraction in the third phases is smaller in extent than that in the "pure" extension-reflex, although it is greater the later ipsilateral stimulation falls. In the fourth phases there is after-discharge of the extensor, and in *e* a late augmentation of it.

This figure demonstrates phenomena very similar to those in the preceding one—which is from the same experiment.

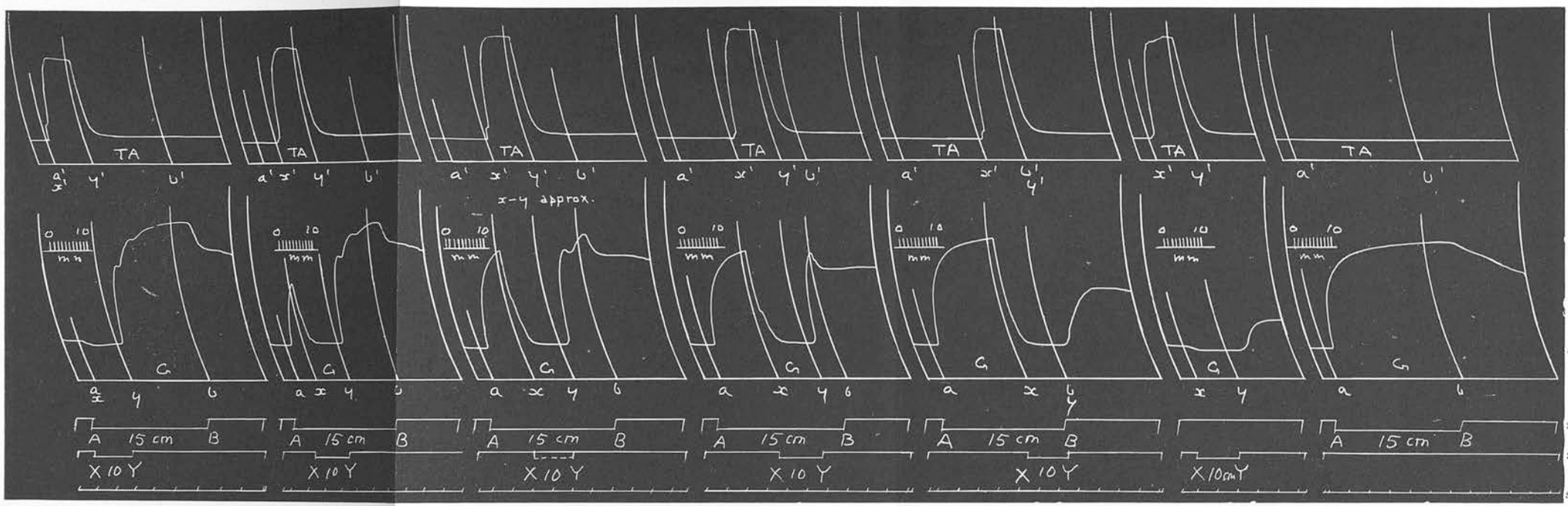


FIG. 14.—Experiment C, clv., record 278, 6601 ; 30/1/13.—Decerebrate cat. A series of compound reactions obtained 2 hours and 42 minutes after decerebration—minute intervals. This record immediately follows (at a minute interval) the last reaction in fig. 15 of the preceding paper. It is immediately followed by the next figure in this paper.

Reaction *f* is a "pure" flexion-reflex—same strength and duration of ipsilateral stimulation as in the compound reactions. Note the extensor rebound contraction of maintained type.

Reaction *g* is a "pure" extension-reflex—note the extension after-discharge. Reactions *f* and *g* may be compared with reactions *a* and *d* of fig. 15 of the preceding paper (xv.) to shew that the reactions in this experiment were of great regularity.

In reactions *a–e* the two stimuli are compounded in different temporal relations, the ipsilateral stimulus falling ever later in the period of the contralateral. During double stimulation complete or nearly complete extensor relaxation occurs, and the flexor contraction which obtains seems to be greater the later the ipsilateral stimulus falls.

In *a*, *b*, and *c* the extensor restitution of contraction, which is the first positive phenomenon in the third phase, is interrupted by one or two "notches." In these reactions it is found that the initial rise of extensor contraction (that is, the rise to the commencement of the "notch") is greater in *b* than in *a*, and in *c* than in *b*. The "notch" seems to be greater the later the ipsilateral stimulus falls. The secondary rise which follows the "notch" carries the level of extensor contraction above that which obtains in the "pure" extension-reflex.

In reaction *d* the contralateral stimulus is withdrawn synchronously with the commencement of the "notch," and no secondary rise occurs.

In the fourth phases of the compound reactions there is an extensor after-discharge which is distinctly of less extent of contraction the later the ipsilateral stimulus falls.

In reaction *e* the two stimuli are synchronously withdrawn. Cessation of stimulation is followed by an extensor rebound contraction of maintained type. This is of much greater extent of contraction than is that in the "pure" flexion-reflex, but not of so great a height as the extensor after-discharge in the "pure" extension-reflex. As this follows complete extensor relaxation during double stimulation, it seems probable that here there is a summation between the extensor rebound conditioned by the flexion-reflex and a central activity which underlies the extensor after-discharge of the extension-reflex.

the ipsilateral stimulus is progressively increased in value in successive reactions.

Where in the "pure" flexion-reflex the extensor rebound is of comparatively long latency—1 second or more—the phenomena of extensor restitution in the third phase are of interest. It then may occur that at first there is a movement of restitution which brings the level of extensor contraction up to that which obtained when the ipsilateral stimulus was applied. This may then be succeeded by a slight relaxation, the commencement of which after the cessation of the ipsilateral stimulus seems to correspond in time with the commencement of the extensor contraction of the rebound in the "pure" ipsilateral flexion-reflex, or to fall in time very slightly before that point. This lasts about 0·2 second–0·25 second only, and then gives place to another phase of increasing extensor contraction. This on completion leaves the muscle in a level of contraction greater than that attained in the "pure" extension-reflex evoked at the same strength of contralateral stimulation. On cessation of the continued contralateral stimulus there may again be a partial relaxation of extensor contraction, which at the end of about 1 second brings the level of contraction to that which obtains in the after-discharge of the "pure" contralateral extension-reflex at the same point after the termination of stimulation [see xv. fig. 15, reaction *c*]. In a record of this nature the curve of restitution of extension in the third phase of the reaction demonstrates an initial rise, a "notch," and a secondary rise. In such an instance the time relations of the two stimuli were progressively changed in successive reactions (fig. 14). It was then found that the initial rise of extensor restitution was smaller the earlier in the period of contralateral stimulation the ipsilateral stimulus was applied (the ipsilateral stimulus was always of a duration of 2 seconds, the contralateral of 6 seconds). The "notch" was greater the later in the period of contralateral stimulation the ipsilateral stimulus fell. The secondary rise was of about equal value throughout the series. In the last but one of the series the contralateral stimulus was withdrawn at the point at which the primary rise terminated and the "notch" commenced. The curve of extensor contraction at once commenced to fall and then shewed no secondary restitution. Having fallen a certain distance, it remained in a tonic extensor after-discharge which was distinctly of less height than in the "pure" extension-reflex. In the earlier members of the series, in which the ipsilateral stimulus fell earlier in the period of contralateral stimulation, and in which there was a greater duration of contralateral stimulation between the cessation of the ipsilateral stimulus and that of the contralateral, the extensor tonic after-discharge on cessation of contralateral stimulation was greater than in the "pure" extension-reflex. When, in the final member of the series, the two stimuli were synchronously withdrawn, there ensued an extensor rebound contraction of shorter latency and greater extent than that in the "pure" flexion-reflex. But this by far did not attain a level as great as that of the extensor after-discharge

in the extension-reflex. It is, however, of interest that in such cases it should be augmented at all. For it seems to point to a summation of the rebound effect and of a central process which underlies extensor tonic after-discharge. If that after-discharge were merely due to the carrying on of the reflex by self-generated proprioceptive impulses, this summation would not be expected to occur in such cases as the present one, where there was complete extensor relaxation at the close of the period of double stimulation; and where, therefore, no such impulses were in course of generation when the two stimuli were withdrawn.

In this same experiment the time relations of the two stimuli were later kept constant and the value of the ipsilateral stimulus was progressively increased in a series of reactions, the value of contralateral stimulation remaining unchanged (fig. 15). Between each pair of the compounded reactions there was registered a "pure" ipsilateral reaction in response to the strength of ipsilateral stimulus used in the following compounded reaction. It was then found that with a subliminal ipsilateral stimulus there yet appeared, on termination of stimulation, an extensor rebound contraction of small extent. When this was compounded with the contralateral extension-reflex there was a certain amount of extensor inhibitory relaxation in the period of double stimulation. On cessation of the ipsilateral stimulus there was a comparatively slow restitution of the extensor contraction. This reached a maximum which was distinctly greater than the level of contraction attained in the "pure" contralateral reaction at the same period after commencement of stimulation. The difference between the two levels was almost exactly equal to the height of the extensor contraction of the extensor rebound phenomenon in the "pure" ipsilateral reaction. As the strength of ipsilateral stimulus was increased the extent of the extensor rebound contraction progressively augmented. In the subsequent compounded reactions there was always an augmentation of extensor contraction in the third phase. The extent of this augmentation (measured as before as the difference in height between the level of contraction in the compounded reaction and the level of contraction after the same duration of contralateral stimulation in the "pure" extension-reflex), however, progressively decreased relatively to the extent of the extensor rebound in the ipsilateral reaction. In the case of the weaker ipsilateral stimuli used the curve of restitution of extension in the third phase was a simple one, and resembled that of the initiation of extensor contraction in the "pure" extension-reflex of "spinal" type. As the strength of ipsilateral stimulation was increased in successive compounded reactions the degree of extensor inhibitory relaxation in the phase of double stimulation became progressively greater. At the same time the restitution of extension became a quicker movement—so that the maximum was reached actually sooner after cessation of ipsilateral stimulation than in the case of the weaker ipsilateral stimuli. At the same time the "notch" appeared as a break upon the curve of restitution. This became more pronounced the

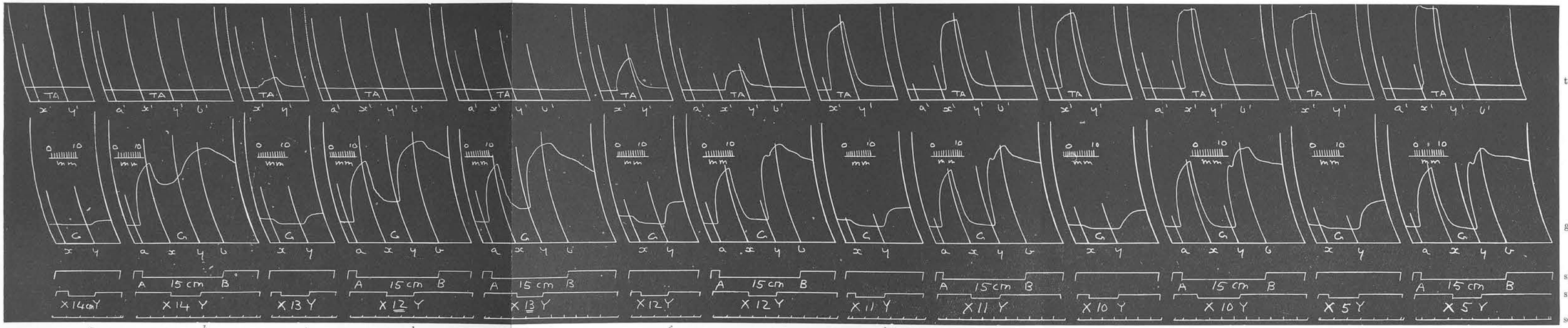


FIG. 15.—Experiment C, clv., record 278, 6608; 30/1/13.—Decerebrate cat. A series of compound reactions obtained 2 hours and 50 minutes after decerebration—minute intervals. This record follows that reproduced in the preceding figure at an interval of 2 minutes.

In this series the temporal relations of the stimuli were constant. Against an extension "background" (see reaction *g* of the preceding figure) different strengths of ipsilateral stimuli are compounded. Between the compound reactions "pure" ipsilateral stimuli are recorded. Note the presence of extensor rebound alone in the weakest of these, and the appearance of flexor contraction accompanied by augmentation of extensor rebound as the strength of ipsilateral stimulus is increased.

In the period of double stimulation note the increase of extensor relaxation with increase in strength of ipsilateral stimulation.

In the third phases of the reactions extensor restitution occurs. This is to a higher level of contraction than that which obtains in the "pure" extension-reflex. This augmentation does not increase in proportion with the increase in the extent of the extensor rebound contraction of the "pure" flexion-reflexes.

In *b*, *d*, and *e* the extensor contraction-curve is a slow and simple one. With further increase in the strength of the ipsilateral stimulus it becomes sharper and a "notch" appears. This becomes more marked the stronger the ipsilateral stimulus is.

stronger the ipsilateral stimulus was. The secondary rise after the "notch" appeared to become greater with increase in the strength of the ipsilateral stimulus (fig. 15).

Still later in this experiment this series of compounded reactions was repeated. Very weak ipsilateral stimulation in the "pure" reaction gave slight ipsilateral extension as a response. Being then compounded with the contralateral stimulus [see xv. fig. 21], there was a distinct augmentation of extension during the period of double stimulation, and a still greater augmentation when the ipsilateral stimulus was withdrawn—although at this strength there was no extensor rebound contraction in the "pure" ipsilateral response. A stronger ipsilateral stimulus in the "pure" reaction gave apparently no movement of either antagonist. When compounded with the contralateral stimulus there was inhibitory relaxation of extensor contraction in the period of double stimulation. This was succeeded by marked augmentation. A yet stronger ipsilateral stimulus when applied "pure" gave no movement of the antagonists during application, but on cessation was followed by the rare "extensor rebound relaxation after inhibition," and this again by an extensor rebound contraction. In the third phase of the compounded reaction there was a slight approximation to a "notch." Further increase in ipsilateral stimulation in the "pure" reaction demonstrated a well-marked inhibitory relaxation of the extensor during stimulation, and a still further relaxation on cessation of stimulation —this again being followed by an extensor rebound contraction. In the extensor restitution of contraction in the third phase of the compounded reaction the "notch" was better marked; and with further increase of the strength of ipsilateral stimulation it became still more evident [see xv. fig. 22].

This case is of interest inasmuch as it shews that the "notch" occasionally seen in these compound reactions is in all probability related to a phenomenon of "extensor rebound relaxation after inhibition" which is not evident as a rule in the "pure" ipsilateral flexion-reflex. A matter of additional interest in this series is the fact that the augmentation of extension in the third phase of the compounded reaction carried the extensor to a level of contraction higher than the summated heights of the "pure" extension-reflex and the extensor rebound contraction in the "pure" ipsilateral flexion-reflex.

In another experiment in which there was present an extensor rebound contraction after the flexion-reflex, the successive effects of double stimulation were carefully examined in series of reactions in which the strengths of stimuli were varied [see xv. figs. 4, 5, 6, 24, 25].

Here, in the first place, against a constant extension "background" varying strengths of ipsilateral stimulation were compounded. The weakest strength used gave an abnormal extension-reflex, and the strongest gave a flexion-reflex of "decerebrate" type followed by an extensor rebound contraction which appeared as a sudden augmentation of the extensor

contraction in being at the end of the 2 seconds of stimulation [see xv. figs. 24, 25]. There here occurred restitution of extensor contraction after double stimulation in the third phase of the compound reaction. This was of very nearly the same level of extensor contraction in the different reactions, but the plateau of maximum contraction in the third phase was reached sooner after the weak interrupting ipsilateral stimuli than after the stronger ones. It must, however, be remembered that the latter produced a greater degree of extensor relaxation during double stimulation than did the former, and that therefore the restitution had to be a larger movement in the latter cases in order to bring the level of contraction up to the same general height from the abscissa. Towards the end of this series very interesting phenomena were observed in the third phases of the compound reactions (fig. 16). Here in the "pure" flexion-reflex withdrawal of the stimulus was followed as before by an extensor rebound contraction. But whereas this had with weaker ipsilateral stimuli been a maintained contraction (and the more perfectly maintained the weaker the stimulus), here it consisted of a sudden contraction which was immediately followed by as sudden a relaxation that brought the level of the extensor contraction to the position of "rest." When this stimulus was compounded in the same manner as before against a contralateral extension "background" there was in double stimulation a greater extensor relaxation than before. On withdrawal of the ipsilateral stimulus there occurred a restitution of extensor contraction which was not quite so great in extent as before (the contralateral "background" had slightly deteriorated and was not quite so strong as before). But the interesting point about the phenomena in the third phase was the fact that after a maximum of extensor contraction had been reached there occurred a phase of relaxation while the contralateral "background" stimulus was still in being. The whole phase of extensor contraction and relaxation in the third phase resembled that of the extensor rebound phenomenon in the "pure" flexion-reflex, but it was of considerably greater extent and longer duration. The lowest point in the movement of relaxation did not bring the extensor to the level of "rest," and it was then immediately followed by a second contraction phenomenon while the contralateral stimulus was still in being. This was of small extent and duration, its smallness being perhaps conditioned by the fact that immediately after its commencement the contralateral "background" stimulus was withdrawn.

The interest of this phenomenon is great. It seems to point to the conclusion that in the terminal phenomena of the flexion-reflex there are (at any rate in such cases) two conditioning antagonistic factors—extension-producing and flexion-producing—and that of these the latter increases in value with increase in the strength of the ipsilateral stimulus. If this be the case, the extensor rebound phenomenon of short duration in the flexion-reflex is explained as due to a foundation of maintained (or "tonic") extensor rebound which is cut short by an antagonistic phenomenon of flexion rebound

(inhibition of extensor contraction here unaccompanied by flexor rebound contraction). The other possible hypothesis is that the extensor rebound of the flexion-reflex, when of short duration, is due simply to a discharge of

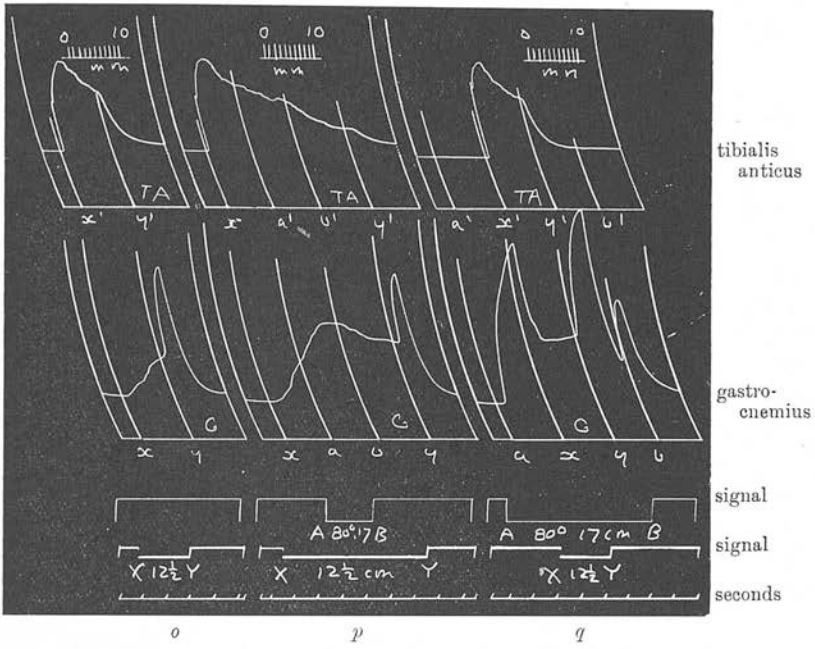


FIG. 16.—Experiment C, clxix., record 300, 7758; 28/2/13.—Decerebrate cat. A series of three reactions obtained 3 hours and 1 minute after decerebration—minute intervals. This series immediately follows that reproduced in fig. 25 of the preceding paper (xv.), and with that figure and fig. 24 in the same paper forms a set of three.

Reaction *o* is a "pure" flexion-reflex. Note the extensor contraction during stimulation, and the extensor rebound contraction on cessation of stimulation. This is of greater extent and less duration than the extensor rebound in the weaker "pure" flexion-reflex (see xv. fig. 25, reaction *e*).

In reaction *p* the compounding is against an ipsilateral flexion "background." The extensor rebound on cessation of the ipsilateral stimulus is smaller than in *a*, but note that the duration of ipsilateral stimulation is of course greater.

In reaction *q* the "background" is extension. Extensor relaxation occurs during double stimulation—note that the level of extensor contraction thus conditioned is slightly less than that during double stimulation in *p*. In the third phase extensor restitution of contraction occurs. This is not so great as that in the corresponding compound reaction where the ipsilateral stimulus is weaker (see xv. fig. 25, reaction *n*). While the contralateral "background" stimulus is still in being extensor relaxation occurs. This is not complete, and the whole movement of extensor contraction and relaxation gives an act of greater extent and duration than the extensor rebound contraction in *o*. It is followed by a secondary extensor contraction, during which the contralateral stimulus is withdrawn. There then follows extensor relaxation. (In the "pure" extension-reflex there was no after-discharge.)

short duration from the extensor "half-centre," and that it is of short duration simply because it "dies away" soon. On this second hypothesis the phenomena in the third phase would be compounded of the extension conditioned by the contralateral "background" stimulus still in being, and the extension of short duration conditioned by the terminal phenomena of the flexion-

reflex. There would therefore be expected to occur a summation of the two extensions only, and no extensor relaxation in the third phase. This is not the case. On the first hypothesis there would be expected to occur in the third phase a summation of the extension conditioned by the contralateral "background" stimulus, and of the extension factor in the terminal phenomena of the flexion-reflex; but this summed extension would be expected to be antagonised in part by the flexion factor in the terminal phenomena of the flexion-reflex. There would therefore be anticipated an augmentation of extensor contraction in the third phase. But this would be expected to be later reduced—at any rate in part—by the flexion factor, which would be expected to condition either a later or a less great relaxation of extension than in the terminal flexion phenomena. In the compound reaction these features were present. There was first extensor augmentation in the third phase, but this was cut short by extensor relaxation. The relaxation occurred later than the corresponding movement in the flexion rebound phenomenon, and it was of less complete extent. There is therefore good ground for the supposition that (at any rate in such cases as these) there is an active factor of flexion in the terminal phenomena of the flexion-reflex, and that this tends actively to cut short the extensor rebound contraction which would otherwise be tonically maintained. And furthermore, there is ground for the supposition that this flexion factor (which may, of course, be evidenced as extension inhibition alone) increases relatively in value with increase in the strength of the ipsilateral stimulus which evokes the flexion-reflex.

In this experiment, and immediately after the reactions described above, a set of three series of reactions was registered (figs. 17, 18, 19). In each of these the interrupting ipsilateral stimulus was kept of constant value (but of different values in the three series) and the values of the contralateral "background" stimulus were progressively increased (the same values being used in the three series). The weakest "pure" ipsilateral stimulus gave an abnormal extension-reflex with little "tonic" extension after-discharge; the medium "pure" ipsilateral stimulus gave flexion of "decerebrate" type and followed by a good extensor rebound of maintained type. In each of the first two series it was found that the extensor restitution in the third phase was greater the stronger the contralateral "background." (Even where the abnormal ipsilateral extension was used there was extensor relaxation during double stimulation.) When these two series were compared together there was found to be—at each strength of contralateral "background" stimulation—a greater extensor restitution of contraction in the third phase when the stronger ipsilateral interrupting stimulus was used. In the final series the values of the contralateral "background" stimuli had somewhat deteriorated. The "pure" ipsilateral stimulus gave a flexion-reflex followed by a marked extensor rebound which again was cut short. In the third phases of the compound reactions there was extensor restitution to a level of contraction greater than that

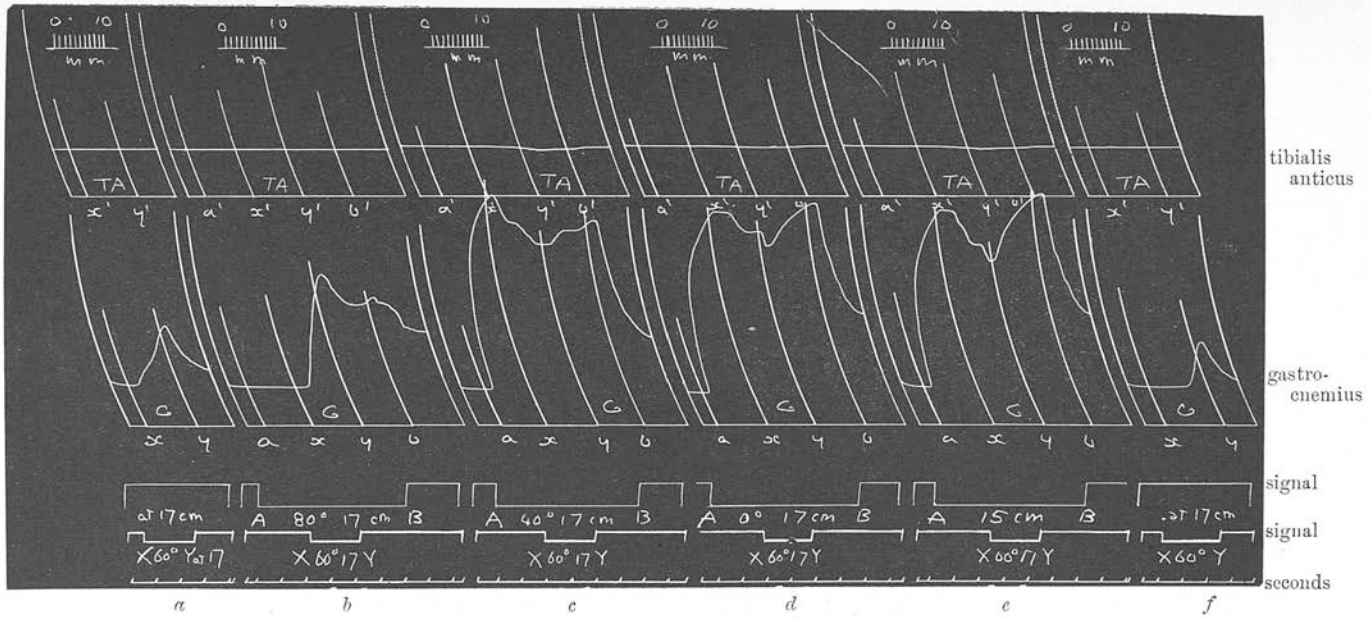


FIG. 17.—Experiment C, clxix., record 300, 7764 ; 28/2/13.—Decerebrate cat. A series of compound reactions obtained 3 hours and 8 minutes after decerebration—minute intervals. This and the two following figures form a set of three series.

Reactions *a* and *f* are "pure" ipsilateral reflexes which demonstrate abnormal direct extension in response to weak stimulation. The strength and duration of stimulation is that used in the interrupting reflex throughout the compound reactions.

Reactions *b*, *c*, *d*, and *e* are compound with extension "backgrounds." The strength of contralateral stimulation is progressively increased. In *b* it is subliminal.

In *b*—subliminal extension "background"—the extensor contraction which appears during double stimulation is of course greater than in the "pure" extension-reflex. In the third phase there persists a certain amount of extensor contraction, and there is an extensor after-discharge in the fourth phase.

In the other compound reactions there is an effective extension "background." During double stimulation there is extensor relaxation, which, on the whole, appears to be greater in *e* than in *c*. Note that this extensor relaxation therefore occurs despite the fact that the interrupting ipsilateral stimulus when "pure" evokes an extension-reflex. In the third phases there is extensor restitution, which is greater the stronger the "background" is. In the fourth phases there is little extensor after-discharge.

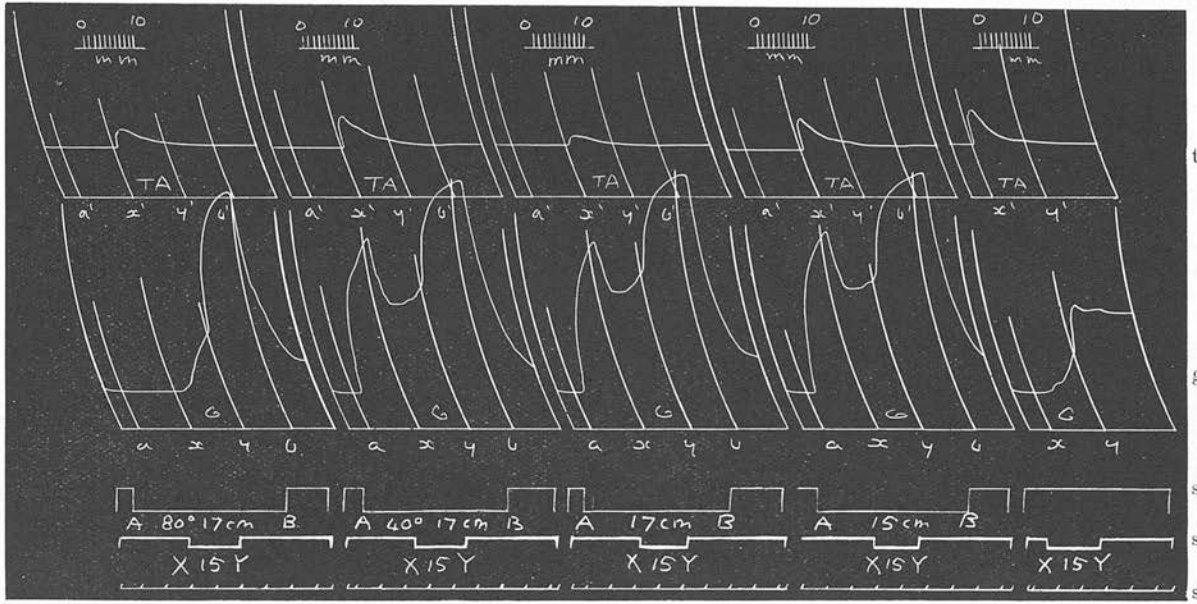


FIG. 18.—Experiment C, clxix., record 300, 7770 ; 28/2/13.—Decerebrate cat. A series of compound reactions obtained 3 hours and 14 minutes after decerebration—minute intervals. This figure immediately follows the previous one in time (an interval of 1 minute between them). It forms the second of a set of three.

Reaction *l* is a "pure" flexion-reflex taken with the strength and duration of ipsilateral stimulation used in the compound reactions. Here the ipsilateral reaction is flexion of "decerebrate" type, and followed by a maintained extensor rebound contraction. The strength of stimulation is greater than in the preceding figure.

Reactions *g*, *h*, *i*, and *k* are compound—the same strengths of contralateral "background" stimulation are used as in the immediately preceding figure.

In reaction *g* the contralateral "background" is subliminal. During double stimulation there is a greater extensor contraction and a less flexor than in the "pure" flexion-reflex. In the third phase there occurs a great augmentation of extensor contraction. This is of much greater extent than the extensor rebound contraction of the flexion-reflex. It is followed in the fourth phases by a slighter extensor after-discharge than in the corresponding reaction *b* of the preceding figure.

In the other compound reactions there is during double stimulation extensor relaxation, which is less the stronger the extension "background" is. In the third phases restitution occurs, and is greater the stronger the "background" is. In the fourth phases extensor after-discharge is less than in the previous figure.

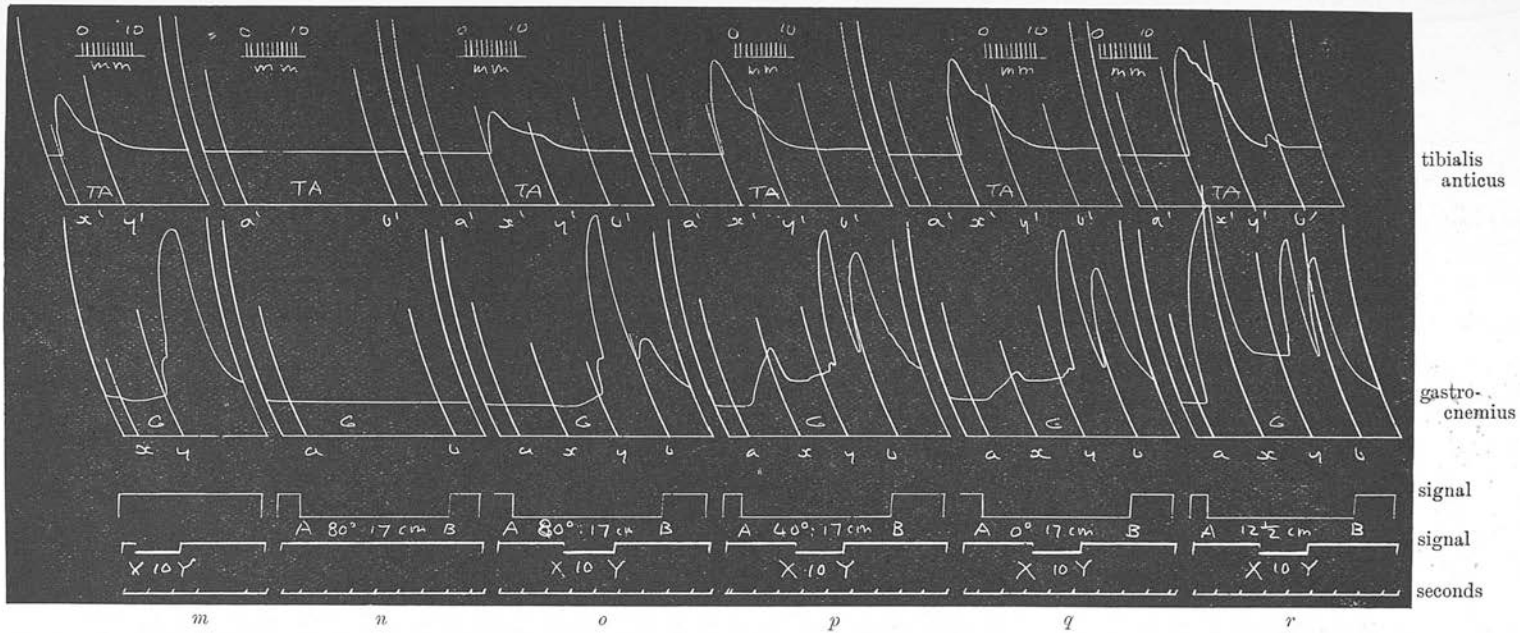


FIG. 19.—Experiment C, clxix., record 300, 7775; 28/2/13.—Decerebrate cat. A series of compound reactions obtained 3 hours and 19 minutes after decerebration—minute intervals. This immediately follows (at 1-minute interval) the previous figure.

Reaction *m* is a "pure" flexion-reflex evoked with the same strength and duration of ipsilateral stimulation as that used in the compound reactions. This strength is greater than those used in the two previous figures. Note that extensor contraction during stimulation is almost absent, and that there is a great extensor rebound contraction which is not maintained—as it is in the previous figure.

Reaction *n* is a subliminal extension-reflex evoked with the same strength of stimulation as that used in reaction *o*.

Reactions *o*, *p*, *q*, and *r* are compound. The strengths of the "background" contralateral stimuli are the same as those used in the two previous figures, with the exception of *r*, which is stronger than *e* and *k*.

In reaction *o* the "background" again is subliminal. During double stimulation there is slight extensor contraction. In the third phase there is an extensor augmentation which is of greater extent but of less duration than is the extensor rebound contraction of the "pure" flexion-reflex. The relaxation phase of this movement occurs during the "background" stimulation, and withdrawal of that stimulus is followed by a second contraction movement.

In the third phases of the other reactions the same phenomenon occurs. The extensor augmentation appears to be of less extent the stronger the "background." The secondary movement appears also to be so. Note that the latency of the extensor augmentation in the third phase appears to be less the stronger the "background" is, and that the secondary extensor movement—considered as an after-discharge—appears also to be less.

in the rebound phenomenon or in the extension-reflex. But again this was cut short during the third phase, and in one instance there even appeared a slight flexor reciprocal contraction.

Yet later in the same experiment another set of three series of reactions was obtained [see xv., figs. 4, 5, 6]. Here the "background" contralateral stimulus was kept of constant value in each series (of different values in the three) and the interrupting ipsilateral stimulus was progressively increased in value in each series (the same values being used in the three series). In this case it was found that in each series the extensor restitution of contraction in the third phase was less the stronger the interrupting ipsilateral stimulus; but in each series there appeared to be a progressive deterioration of the value of the "background" contralateral stimulus. What was of particular interest was a comparison of the three end reactions in each series. Here the ipsilateral stimulus (comparatively strong) was of the same value; but the "background" stimulus was of different values. The "pure" ipsilateral stimulus gave a flexion-reflex followed by an extensor rebound contraction of short duration. When compounded against the weakest contralateral "background" (then probably subliminal) there was actual augmentation of this rebound contraction, but then a phase of relaxation occurred during the third phase. The whole movement was, however, of greater duration than in the rebound phenomenon of the "pure" flexion-reflex, and it was followed—on cessation of the contralateral stimulus—by a flexor rebound contraction which was not present in the flexion-reflex. Against the medium contralateral "background" in the third phase there was a still greater augmentation of extension. Again, there was extensor relaxation during the third phase, but this was followed by a slight restitution. The contralateral stimulus being cut off, this restitution was a slight movement and was followed by another flexor rebound contraction which was of greater extent, but also of greater latency, than before. Against the strongest contralateral "background" used there was a greater degree of extensor restitution of contraction in the third phase than before—but it cannot be said whether there was actual augmentation or not. There was here no extensor relaxation during the third phase, and the cessation of contralateral stimulation was followed by an extensor after-discharge which was cut short by relaxation in about 0·75 second after the end of the contralateral stimulus. This was followed in time by a reciprocal flexor rebound contraction which was smaller and of greater latency than before.

The phenomena here confirm the above hypothesis, for it would be expected that the stronger the extension "background" the less would be the effect of the antagonistic flexion rebound factor. Therefore it would be expected that with a strong extension "background" the factor of flexion (or of extension inhibition) would be completely suppressed—and this, in fact, is the case.

### 3. In Cases in which both Flexor Rebound Contraction and Extensor Rebound Contraction are present in the Flexion-Reflex.

In a few experiments in which the antagonistic stimuli have been compounded in the manner here described the ipsilateral flexion-reflex has been followed by both "flexor rebound contraction after excitation" and "extensor rebound contraction after inhibition." When these occur together they are almost always arranged in temporal succession. Most commonly in these circumstances the first terminal phenomenon to succeed cessation of stimulation in the flexion-reflex is a flexor rebound contraction, and when this dies away there appears an extensor rebound contraction of maintained type. This course of events seems to occur when the flexor rebound contraction is of great extent and of relatively great duration, and also when it occurs soon after cessation of stimulation. If the flexor rebound is delayed—and then it usually is of comparatively short duration —the first phenomenon to appear is the maintained extensor rebound. This is cut down during the flexor rebound, but is thereafter usually reconstituted and continues as the usual maintained extensor contraction. In any case it is common for the final phenomenon to be the maintained extensor contraction.

In one experiment [see xv., fig. 3] there had previously in the "pure" flexion-reflex been a flexor rebound contraction followed by a maintained extensor rebound. The rebound phenomenon was sometimes rhythmic [see ix., fig. 25]. Later in the experiment the flexor rebound phenomenon was absent; but in the third phase of the compound reactions, in which the extension reaction served as the "background," there was a distinct "notch" in the curve of extensor restitution when double stimulation fell early in the course the contralateral stimulus. When it was applied later the notch was greater and there appeared a slight flexor rebound contraction in the third phase. When both stimuli were synchronously commenced and terminated there appeared a good flexor rebound contraction on cessation of double stimulation. This was not then present in a "pure" ipsilateral flexion-reflex taken with the same strength of stimulation but with a shorter duration of stimulus.

In another experiment [see xv., fig. 13, reaction *a*] no flexor rebound occurred in response to a "pure" ipsilateral stimulus of the strength and duration subsequently used in a compound reaction, but there was an extensor rebound contraction of short duration—that is, one which was cut short (this was not reproduced in the figure mentioned). With a rather stronger stimulus the ipsilateral reflex (reproduced in that figure) was followed first by an extensor rebound contraction. This was cut short by a relaxation which was reciprocal to a flexor rebound contraction of small size and short duration. Thereafter the extensor rebound was reconstituted and remained as a maintained contraction. The third phase of

the compound reaction shewed an incompletely rhythmic phenomenon. There was little extensor restitution of contraction, but a certain amount of extensor contraction remained in continuation of a late extensor contraction which had appeared during the phase of double stimulation. This was rhythmically varied, and in the flexor curve there were reciprocal contractions and relaxations. These were two in number. The first was small, but the second was considerably larger than the flexor rebound contraction of the somewhat stronger "pure" flexion-reflex.

In a third case there was, at one time, a great flexor rebound contraction in the "pure" flexion-reflex. This was followed by a late extensor rebound contraction of maintained type. In a compound reaction there was, during double stimulation, an augmentation of flexor contraction. On withdrawal of the ipsilateral stimulus there was a flexor rebound in the third phase. This was of less height but of better maintenance than that of the "pure" reflex. There was no extensor restitution in the third phase, and the flexor contraction gave place to relaxation while the contralateral stimulus was still in being.

Later in this same experiment (fig. 20) the flexor rebound had disappeared in the flexion-reflex, and the only terminal phenomenon was a well-marked maintained extensor rebound contraction. Here the two stimuli were compounded in a series of reactions in which their temporal relations were changed. During double stimulation there was flexor augmentation, and this was found to be greater the later the ipsilateral stimulus fell in the period of the contralateral. When it fell early there was no flexor rebound contraction in the third phase, but in the reactions in which the ipsilateral stimulus was commenced some time after the commencement of the contralateral "background" stimulus such a flexor rebound appeared. This seemed upon the whole to be greater the later the ipsilateral stimulus fell. It was followed by extensor restitution of contraction towards the end of the third phase, and this brought the muscle to a level of contraction which was greater than that in the "pure" contralateral extension-reflex but less than that in the maintained extensor rebound in the "pure" flexion-reflex.

In a fourth experiment (fig. 21) [see also xvii., fig. 15] there was a flexor rebound contraction in the "pure" flexion-reflex. This was preceded by the appearance of the extensor rebound, and after the flexor rebound had disappeared the extensor rebound was reconstituted and remained in maintained contraction. In a compound reaction there was, in the third phase, at first a very slight extensor restitution of contraction. This again gave place to relaxation at about the point at which the flexor rebound would have been expected to have appeared, but no flexor rebound contraction was present during the third phase of the compound reaction. Later in the experiment the flexor rebound had disappeared, and cessation of stimulation in the "pure" ipsilateral reflex was almost immediately followed by an extensor rebound contraction of maintained type. In a

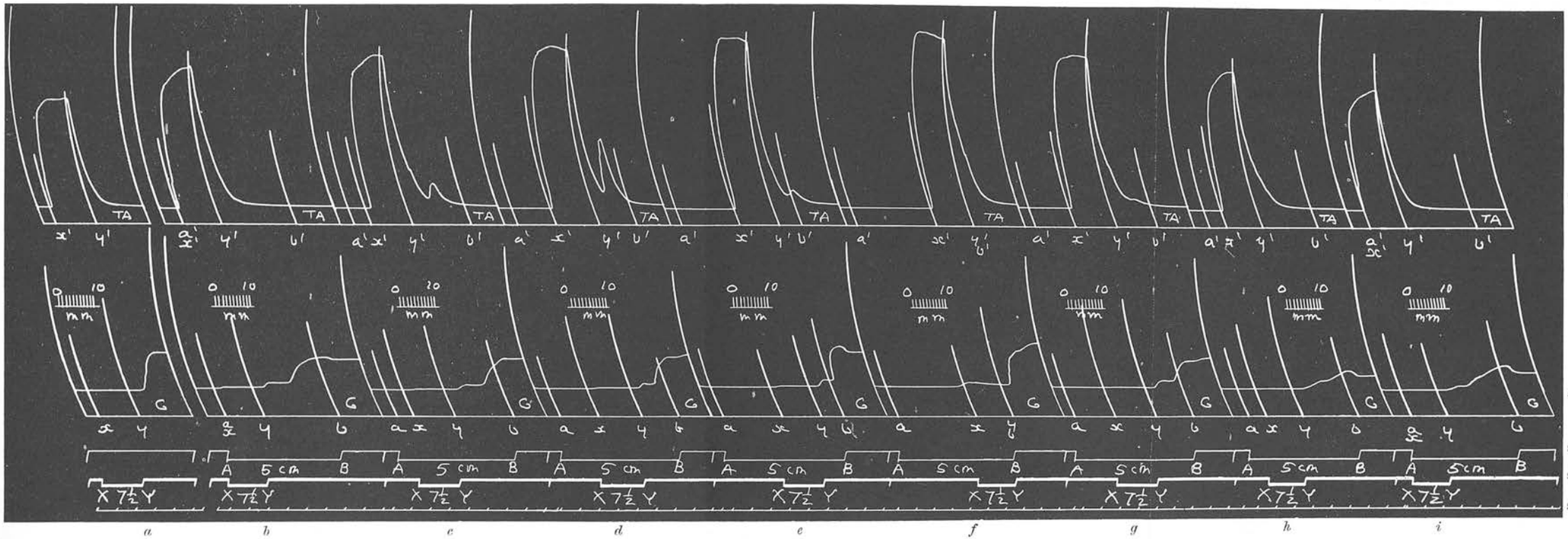


FIG. 20.—Experiment C, clviii., record 283, 6872 ; 11/2/13.—Decerebrate cat. A series of compound reactions obtained 2 hours and 38 minutes after decerebration—minute intervals.

Reaction *a* is a "pure" flexion-reflex obtained before the series of compound reactions and at the strength of ipsilateral stimulation used in them. In the terminal phenomena there is an extensor rebound contraction only.

Reactions *b*–*f* are compound. The contralateral stimulus is subliminal, and the ipsilateral is applied at different points in the period of the contralateral. The strengths of the two are unaltered throughout. In reactions *g*–*i* the temporal relations of the two stimuli are changed in the reverse order—$g=d$ ; $h=c$ ; $i=b$.

In the phases of double stimulation there occurs flexor contraction which is greater than in the "pure" flexion-reflex, and appears to be greater the later the ipsilateral stimulus falls in the period of the contralateral "background." In the third phases of the compound reactions a flexor rebound contraction occurs. On comparing *b*, *c*, and *d* this appears to be greater the later the ipsilateral stimulus falls. Later in these phases extensor contraction occurs. This is "notched" reciprocally to the flexor rebound, but the "notch" appears when there is no flexor rebound. The extensor contraction is not of so high an extent as that of the extensor rebound in the "pure" flexion-reflex. In the fourth phases there is extensor after-discharge. In *f*—where the two stimuli are synchronously terminated—there is an extensor rebound contraction which is of shorter latency than that in the "pure" flexion-reflex.

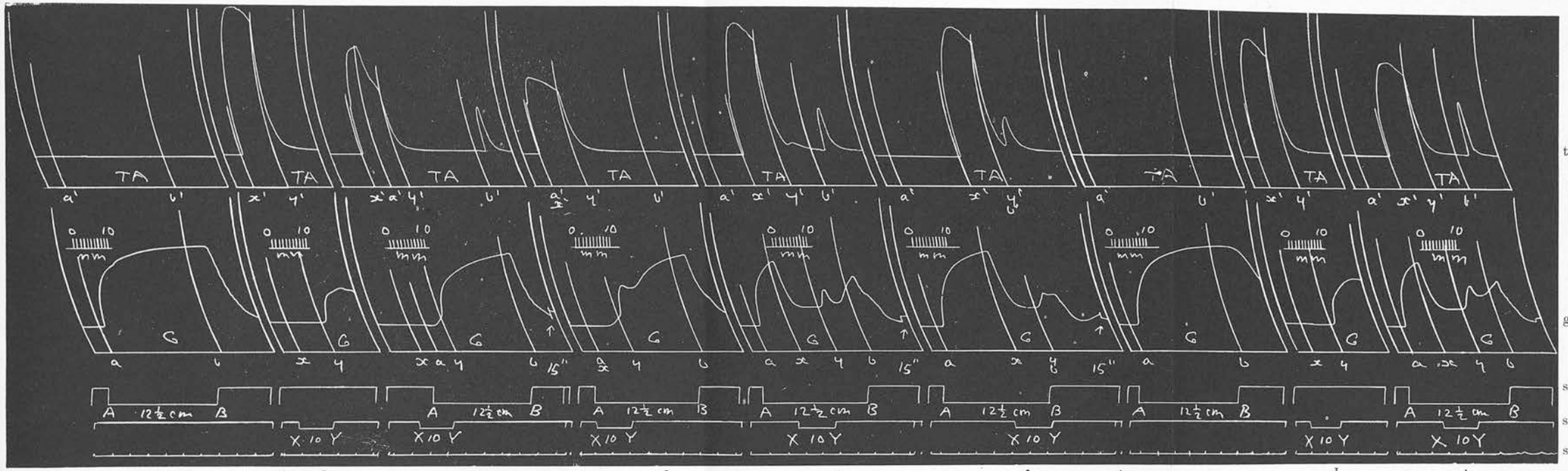


FIG. 21 —Experiment C, clxx., record 302, 7920 ; 3/3/13. Decerebrate cat. A series of compound reactions obtained 3 hours and 29 minutes after decerebration—minute intervals. [This series follows that reproduced in xvii. fig. 21 directly in time—one minute interval between the last reaction there and the first here. A comparison of the two figures demonstrates the differences in the periods of double stimulation when different "backgrounds" of varying previous durations are used. The stimuli are of the same strengths throughout.]

Reactions *a* and *g* are "pure" extension-reflexes—observe the extensor relaxation on cessation of stimulation.

Reactions *b* and *h* are "pure" flexion-reflexes—observe the maintained extensor rebound contraction.

Reactions *c*-*f* and *i* are compound. The strengths of the two stimuli are the same as those used in the "pure" reactions, but their temporal relations are changed—the ipsilateral stimulus falling ever later in the period of the contralateral.

During the phases of double stimulation there is a flexor contraction which is greater the later the ipsilateral stimulus falls in the period of the contralateral. At the same time the extensor depression is, however, less.

In the third phases of the compound reactions there occurs extensor restitution. This is not to the same level of extensor contraction that obtains during stimulation in the "pure" extension-reflex. Where the period of double stimulation falls very early [reaction *c*, the ipsilateral stimulus is there first applied and first withdrawn, and the period of double stimulation is of 1 second duration only] the curve of extensor restitution is a simple one. Where it falls later [reaction *d*, duration of double stimulation 2 seconds—as in all the other compound reactions] there is a "notch," but the curve of flexor relaxation is a simple one. Where it falls still later [reactions *e* and *i*] the "notch" is a larger one. At the same time [*e*] there appears a slight flexor rebound contraction within the third phase and reciprocal to the "notch." At the end of the series the temporal arrangements of reaction *e* are repeated in reaction *i* with almost identical results as regards the curve of the extensor. In the flexor the slight restitution during the third phase ("rebound") is, however, absent.

In the fourth phases of the compound reactions there is flexor rebound contraction which is present in neither "pure" reflex. In *f*—where the two stimuli are synchronously withdrawn—note that there is a slight extensor rebound contraction, which soon gives place to relaxation. It is much less in extent than either the extensor rebound of the "pure" flexion-reflex or the extensor after-discharge of the extension-reflex. There also here appears a flexor rebound contraction, although present in neither "pure" reflex. It gives a slight "notch" on the extensor rebound.

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series of compound reactions the temporal arrangements of the antagonistic stimuli were altered. During the phase of double stimulation there was flexor depression, but the element of flexor contraction during double stimulation was greater the later double stimulation fell in the period of the "background" contralateral stimulus. At the same time, as sometimes happens, the element of extensor relaxation during double stimulation was less the later the period of double stimulation fell. In the third phases of the compound reactions a marked restitution of extensor contraction took place. This was greater the earlier double stimulation fell. When the period of double stimulation was only 1 second, and fell at the commencement of the period of contralateral stimulation (in reality the ipsilateral stimulus was here commenced first, although the contralateral was left in action on withdrawal of the ipsilateral), the extensor restitution of contraction was greatest, and it was of an uncomplicated outline—like that of the phase of increasing contraction in the "pure" extension-reflex of "spinal" form. But where the period of double stimulation was one of 2 seconds, the course of restitution of extensor contraction in the third phase of the reaction was interrupted by a partial relaxation. This soon passed over again into contraction while the contralateral stimulus was still in being. When the period of double stimulation fell later, there was a greater "notch" in the curve of extensor restitution in the third phase, and this was accompanied by a reciprocal flexor contraction. When the two stimuli were synchronously stopped this flexor rebound was also seen. At the end of the series it was again absent in a "pure" flexion-reflex. It is noteworthy that in the "pure" extension-reflex there was terminal relaxation and little "tonic" after-discharge.

### B. Successive Phenomena after the Discontinuation of the Contralateral Extension-Reflex ["Fourth Phase" of the Compound Reaction].

Discontinuation of the contralateral extension-reflex in the decerebrate preparation is most commonly followed by a "tonic" after-discharge of the extensor muscle, but this is only one of the terminal phenomena which may occur. In the first place, cessation of contralateral stimulation may be followed by an increase of extensor contraction—the comparatively rare "extensor rebound contraction after excitation." This may be an augmented contraction of long or of short duration. Secondly, there may occur the usual extensor after-discharge—which carries on the level of contraction which obtained at the end of the period of stimulation. Thirdly, there may occur a greater or a less relaxation of the extensor contraction. This is an "extensor rebound relaxation after excitation," and it seems to be related to a flexor rebound contraction which, however, may be suppressed. Fourthly, there may be a "flexor rebound contraction after inhibition" which accompanies this extensor relaxation. In

the two latter cases the extensor relaxation may be final—that is to say, that there may be no secondary restitution of the extensor after-discharge. But sometimes such a restitution occurs, and when this is the case, the extensor after-discharge is, as it were, reconstructed and then dies slowly away in the usual manner.

Of these four varieties of extension terminal phenomena we have already considered the second as modified in compound reactions where the contralateral "background" stimulus is continued after the cessation of the period of double stimulation.

### 1. Where "Extensor Rebound Contraction after Excitation" is present in the "Pure" Extension-Reflex.

The rare "extensor rebound contraction after excitation" has occasionally occurred in "pure" extension-reflexes which later were compounded with ipsilateral flexion (fig. 3). In no case, however, has it been very well marked. In the compound reaction the extensor rebound contraction may still appear on withdrawal of the contralateral stimulus. Although in some cases there has been a slight indication that this was of greater extent than in the "pure" contralateral extension-reflex, in other cases there has appeared to be a certain depression of it, and it may even be absent.

### 2. Where "Extensor Rebound Relaxation after Excitation" is present in the "Pure" Extension-Reflex.

This phenomenon, which may be looked upon as an incomplete form of the flexor rebound contraction accompanied by reciprocal extensor relaxation in the extension-reflex, has occurred in many experiments in which the two antagonistic stimuli were compounded with the extension-reflex as "background." The extent of the phenomenon has varied from a comparatively slight relaxation, after which the maintained extensor after-discharge is carried on at that level, to a complete depression, after which there is no further maintained extensor contraction.

If, in the first place, attention is directed to those experiments in which the extensor relaxation on cessation of stimulation in the "pure" extension-reflex was slight, it is found that upon the whole there is a greater extent of extensor relaxation after stimulation in the compound reaction than in a "pure" extension-reflex of the same strength and duration of stimulation as the contralateral "background" stimulus there. This relaxation, although greater than that in the "pure" reflex, may yet be incomplete—so that a certain degree of extensor after-discharge continues. This increase in the amount of relaxation is seen in cases where the restitution of extensor contraction in the third phase of the reaction is complete—that is to say, when the level of contraction attained is equal to that which obtains at the same period after the commencement of the evoking

stimulus in the "pure" reflex. It is also seen when there is augmentation of the extensor restitution, and also when the extensor restitution of the third phase is incomplete. A comparatively slight extensor relaxation may be present in the "pure" reaction, and yet there may be complete relaxation of extensor contraction in the fourth phase of the compound reaction (fig. 22). In another case in which this was seen the relaxation in the compound reaction was a sharp movement but not a complete

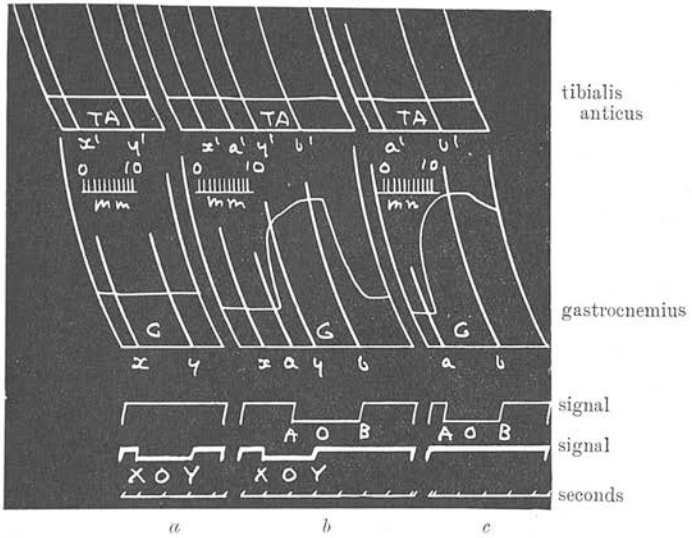


FIG. 22.—Experiment C, clxiv., record 293, 7341; 20/2/13.—Decerebrate cat. Three reactions obtained 2 hours and 36 minutes after decerebration—minute intervals.

Reaction *a* is a "pure" ipsilateral one. It is really a just liminal abnormal ipsilateral extension, and earlier in the experiment the extension had been more clear.

Reaction *c* is a "pure" contralateral one. Note the slight extensor terminal relaxation.

In reaction *b* the two are compounded in "step" arrangment. Ipsilateral first, then contralateral added, then ipsilateral withdrawn, then contralateral withdrawn. Note in the third phase a slight flattening of the curve of extensor contraction. In the fourth phase—that is, after withdrawal of the contralateral stimulus—there is a complete extensor relaxation. The effect of the previous ipsilateral flexion-producing stimulus is to convert a partial terminal extensor relaxation into a complete one. Both before and after this compound reaction the "pure" extension-reflex was always followed by a well-marked extensor after-discharge, and that in reaction in *c* here is not so well marked as was usual—in other words, the extensor rebound relaxation in *c* is greater than was usual.

one. It was followed by a restitution of the maintained extensor after-discharge.

Where the extensor terminal relaxation in the "pure" extension-reflex is of medium extent there is usually a complete extensor relaxation in the compound reaction. This may occur where during the greater part of the third phase of the reaction there is continued extensor depression. Thus in one instance this occurred—the phenomenon was incompletely rhythmic,—but just at the close of the phase there was a sudden restitution of extensor contraction. On withdrawal of the contralateral "background" stimulus there was a sudden and complete relaxation of extensor contraction, although

in the "pure" extension-reflex there was a considerable extensor after-discharge [see xv., fig. 13]. In one experiment the temporal relations of the two stimuli were varied (fig. 8). It was found that the extensor relaxation in the fourth phase of the compound reaction was incomplete when double stimulation fell early in the period of the contralateral "background" stimulus, and that it was the more complete the later it fell. When double stimulation was very early there remained a considerable extensor after-discharge on withdrawal of the contralateral stimulus; if it fell somewhat later there was a sharper and greater relaxation, but this was followed by a slight restitution; when double stimulation fell still later there was a more complete relaxation which was not followed by restitution; and when the two stimuli were synchronously terminated there was a very slight extensor rebound from the level of the nearly complete relaxation which obtained during double stimulation, but this passed over into complete relaxation within 0·5 second. At the end of the series the double stimulation was again placed early in the period of the contralateral stimulus, and again the extensor terminal relaxation was smaller. The phenomenon of its variation with the temporal variation of the stimuli was therefore not attributable to "fatigue" or to some central change unconnected with that temporal variation In another experiment the strengths of the antagonistic stimuli were varied. Here the terminal relaxation of extensor contraction in the compound reaction appeared to be greater and more rapid the stronger the ipsilateral interrupting stimulus [see xv., figs. 4, 5, 6, 25]. With a weak ipsilateral stimulus there was here a reaction of abnormal extension, and when this strength of ipsilateral stimulation was used there appeared to be a decrease in the extent of the extensor relaxation in the fourth phase of the compound reaction [see xv., fig. 24]. In this experiment it was particularly remarkable that with strong ipsilateral stimuli there was not only a greater extensor relaxation in the fourth phase, but there appeared, in addition, a flexor rebound contraction which was present neither in the "pure" ipsilateral flexion-reflex nor in the "pure" contralateral extension-reflex [see xv., figs. 4, 5, 6].

Where the extensor relaxation is of complete extent in the "pure" extension-reflex, the extensor relaxation of the fourth phase of the compound reaction usually is a more rapid movement, and of earlier occurrence, than that of the "pure" extension-reflex. At the same time it is usually accompanied by a flexor rebound contraction which is not present in the "pure" extension-reflex. On two occasions when this phenomenon occurred the stimuli were changed in temporal relationship in series of reactions. It was then found (fig. 21) [see also xv., fig. 16] that upon the whole the flexor rebound was greater the later the double stimulation fell in the period of the extension-reflex. In both experiments there was only a maintained extensor rebound in the "pure" flexion-reflex, but when the two stimuli were synchronously withdrawn there appeared a flexor rebound contraction.

3. Where "Extensor Rebound Relaxation" is accompanied by "Flexor Rebound Contraction" in the Terminal Phenomena of the Contralateral Extension-Reflex.

Where this occurs the phenomenon may be regarded as the complete form of which the extensor relaxation when it occurs alone is an incomplete aspect. In almost every case there has been observed to be an augmentation of the flexor rebound contraction of the compound reaction when compared with that which follows "pure" contralateral stimulation of the same strength and duration as that used for the "background" of the compound reaction. In two cases the values of the interrupting ipsilateral stimuli were progressively increased in series of reactions—the contralateral "background" remaining of constant value, and the temporal relations of the two stimuli being in all cases the same. In each of these two cases it was found that the extent of the flexor rebound contraction increased with increase in the strength of the interrupting ipsilateral stimulus. At the same time the reciprocal extensor relaxation became ever a more sudden movement, and occurred at ever shorter intervals of time after the cessation of the contralateral "background" stimulus. In the preceding third phase of the compound reaction there was nearly complete extensor restitution. This attained nearly to the same level in every case, but was slightly lower in level the stronger the interrupting ipsilateral stimulus. "Pure" contralateral reactions taken before and after the series gave almost identical responses, but the flexor rebound was smaller after the series than before it. When the temporal relations of the compounded stimuli were varied the results obtained were not very constant. In once instance there was indication that the flexor rebound was of greater extent the later the ipsilateral stimulus fell in the period of the contralateral "background." In another case the reverse appeared to be the case, but in this instance the value of contralateral stimulation deteriorated throughout the series, although the strength of the contralateral stimulus was constant. In a few instances the flexor rebound after the compound reaction has been observed to be smaller than that in the "pure" contralateral reaction. In many of these cases in which flexor rebound augmentation has been observed in the compound reaction there has been a flexor rebound in the "pure" flexion-reflex as well as in the "pure" contralateral extension-reflex.

## VII. Conclusions and Summary.

1. Where the two antagonistic stimuli are synchronously terminated, and where there is no rebound phenomenon in the "pure" flexion-reflex and only extensor after-discharge in the "pure" extension-reflex, there often occurs extensor relaxation on withdrawal of the two stimuli. Complete suppression of extensor after-discharge may occur in those cases in which there is complete extensor suppression during double stimulation.

Where complete extensor suppression does not occur during double stimulation there may yet occur extensor relaxation on synchronous termination of the two stimuli. An incomplete extensor after-discharge may occur. This has been observed to be diminished if the strength of the ipsilateral stimulus is increased, and to be increased if the contralateral stimulus is first applied late in the period of the ipsilateral stimulus—both stimuli being synchronously withdrawn. The later the contralateral stimulus is applied the greater is the extent of the extensor after-discharge. It is possible that this phenomenon of suppression (either partial or complete) of extensor after-discharge points to the flexor relaxation, which is the terminal phenomenon in these flexion-reflexes, as an active phenomenon and not merely as a passive one.

2. Where flexor rebound contraction occurs as a terminal phenomenon in the contralateral extension-reflex and the two antagonistic stimuli are compounded there seems usually to occur an augmentation of that rebound on synchronous withdrawal of the two stimuli. In the section in which these phenomena are described there is instanced a curious case of reversal of the contralateral reaction to abnormal flexion when the contralateral stimulus is applied in time shortly after an ipsilateral.

3. Where flexor rebound contraction occurs in the "pure" ipsilateral flexion-reflex as a terminal phenomenon, and where the "pure" contralateral extension-reflex is followed by an extensor after-discharge, there may appear a depression of the flexor rebound as the terminal phenomenon in a compound reaction in which the stimuli are synchronously withdrawn. But where in the "pure" extension-reflex extensor relaxation has appeared as the terminal phenomenon, there has been observed to be augmentation of the flexor rebound contraction. Perhaps these two observations may be reconciled on the hypothesis that in the terminal phenomena of the compound reactions in the two cases there is a compounding of the factors present in the terminal phenomena of the "pure" reactions. Thus in the one case they are antagonistic—flexor rebound and extensor after-discharge —and the compound terminal phenomena shew algebraic summation of the two; while in the other case the two phenomena are not antagonistic, and augmentation of the common terminal phenomenon (flexor contraction: extensor relaxation) occurs.

4. Where in the "pure" reflexes there is flexor rebound in both, synchronous withdrawal of the two stimuli seems to be followed by an augmentation of the flexor rebound—so that it is greater either in extent or duration than that in either "pure" reflex.

5. Where the "pure" ipsilateral flexion-reflex is not followed by any terminal phenomenon save flexor relaxation, and where there is extensor after-discharge in the contralateral extension-reflex, on synchronous withdrawal of the two stimuli in a compound reaction there may ensue an extensor rebound when during double stimulation there is complete suppression of extensor contraction. Where there is incomplete suppression

there may ensue an augmented extensor after-discharge. In some cases this rebound or after-discharge has been observed to be greater than the after-discharge of the "pure" extension-reflex in extent; but more commonly it is of less extent.

6. Where extensor rebound contraction occurs in the "pure" flexion-reflex, and extensor after-discharge in the "pure" extension-reflex, in compound reactions there may occur augmentation of the extensor terminal phenomenon on synchronous cessation of the two stimuli. The extent of extensor contraction in the terminal phenomena of the compound reaction may be greater than the sum of the extents of the extensor terminal phenomena in the "pure" reflexes. In other cases depression of the extensor terminal phenomenon may occur. In series of "pure" flexion-reflexes evoked with increasing strengths of ipsilateral stimuli the extensor rebounds may be found to decrease in value. In these circumstances, if series of compound reactions in which the strength of ipsilateral stimulation is increased progressively are recorded, it is found that with weak ipsilateral stimuli the extensor rebound is augmented, but that with strong ipsilateral stimuli it is depressed or even abolished—although there is a good extensor after-discharge after cessation of the "pure" contralateral stimulus of the constant value used throughout the series. Again, in such cases the extensor rebound after cessation of double stimulation may be found to be greater the greater the duration of a preceding contralateral extension "background" when the contralateral stimulus is commenced in time before the ipsilateral, but the two are synchronously withdrawn. Here it may be noted that the extensor after-discharge may in these cases be greater the longer the duration of the "pure" contralateral stimulus.

7. In compound reactions in which the ipsilateral interrupting stimulus is withdrawn before the termination of the contralateral extension "background" there occur two phases in which the terminal phenomena of compound stimulation may be examined. The first of these is the "third phase" of the compound phenomenon; in it the "background" extension stimulus is still running—it commences at the point at which the ipsilateral interrupting stimulus is withdrawn, and terminates with the withdrawal of the contralateral "background" stimulus. The second is the "fourth phase" of the compound reaction; in it there is no stimulus in being—it commences with the withdrawal of the contralateral "background" stimulus, and may be held to terminate when the centres again assume the condition of "rest."

8. Where the "pure" ipsilateral reflex is not followed by any rebound contraction—but only by terminal flexor relaxation—the "third phase" of the compound reaction (extension "background") is usually characterised by a flexor relaxation more rapid than in the "pure" flexion-reflex, and by a reconstitution of extensor contraction which is more slow, and less regular, a movement than that at the commencement of the "pure" extension-reflex.

The extent of extensor contraction attained is in some cases greater than that in the "pure" extension-reflex, but it is usually less.

9. When the time relations of the two stimuli are changed it is found in these cases that the extent of extensor restitution in the third phase is usually greater the later the ipsilateral stimulus falls in the period of the contralateral "background." At the same time the curve of extensor restitution appears as a sharper movement the later the ipsilateral stimulus falls.

10. When the strengths of the two stimuli are relatively varied in compound reactions in which the time relations of the stimuli are kept constant, it is found that in some cases the extensor restitution of the third phase is greater the stronger the ipsilateral flexion-producing stimulus. In other cases it is weaker. In one case it became stronger, reached a maximum, and then declined as the ipsilateral stimulus was progressively increased in value. In the other cases the series examined may have been "partial" ones only—either above or below the optimum.

11. In the "fourth phase" of compound reactions, where the "pure" ipsilateral stimulus is followed by flexor relaxation alone, there may continue an extensor after-discharge if that be present in the "pure" extension-reflex. This carries on the extensor at the level of contraction attained in the third phase. But sometimes extensor relaxation occurs. When this is the case and the temporal relations of the two stimuli are varied, it is found that the depression of extensor after-discharge is greater the later the ipsilateral stimulus falls (that is, in these cases, the shorter the period of the third phase).

12. Where "flexor rebound contraction after excitation" is present in the "pure" ipsilateral flexion-reflex, it may also appear in the third phase of compound reactions. Here there then appears to be a summation of the flexion factors of the ipsilateral terminal phenomenon and the extension factors of the continued "background" extension-reflex—for the flexion rebound in the third phase may be smaller than that in the "pure" flexion-reflex, and the extensor contraction in the third phase may be depressed. But it occasionally happens that a flexor rebound may appear in the third phase when not present after the same duration of stimulation in the "pure" flexion-reflex. In an instance in which this occurred it was found that the flexor rebound was smaller the later the ipsilateral stimulus fell in the period of the extension "background." Where extensor restitution begins to occur during double stimulation there is a marked extensor relaxation at the commencement of the third phase reciprocal to the flexor rebound.

13. Where "extensor rebound contraction after inhibition" is present in the "pure" flexion-reflex the phenomena in the third phases of compound reactions are of interest. Thus in some cases it may occur that there is a depression of extensor restitution in the third phases even in these circumstances. But more usually there appears an augmentation.

The level of extensor contraction then attained in the third phase may be greater than the summed extents of extensor contraction in the "pure" extension-reflex and in the extensor rebound of the "pure" flexion-reflex. A point of interest is the appearance of a notch-like relaxation of extensor contraction during the third phase. This has appeared in instances in which there appeared in the terminal phenomena of the flexion-reflex an "extensor rebound relaxation after inhibition" followed by an extensor rebound contraction. The phenomenon has appeared in the compound reaction when not present in the flexion-reflex at that strength of stimulus.

14. Where the temporal relations of the stimuli are varied and such a "notch" appears, it has been found that it was larger the later the ipsilateral stimulus fell in the period of the contralateral "background" stimulus. The primary movement of extensor restitution in the third phase was found to be sharper the later that stimulus fell, but little variation was observed in the secondary extensor contraction which followed the "notch."

15. Where the temporal relations of the stimuli are constant but their values changed, the level of extensor contraction in the third phase may be found to augment with increase in the value of the ipsilateral stimulus. In such cases it is found that the extensor rebound contraction of the "pure" flexion-reflex increases with increase in strength of stimulus. The extensor contraction in the third phases of the compound reactions is greater than that in the "pure" extension-reflex. With weak ipsilateral stimuli the difference between the levels of extensor contraction in the extension-reflex and in the third phase of the compound reaction may be equal to, or even greater than, the extent of extensor contraction in the extensor rebound contraction of the flexion-reflex. But with stronger ipsilateral stimuli this relative difference of extent becomes smaller than the extent of the extensor rebound in the corresponding flexion-reflex—although the absolute extent of extensor contraction in the third phase continues to increase. The "notch"—if present—may be greater the stronger the ipsilateral stimulus. Where the ipsilateral stimulus is of constant strength and the contralateral "background" stimulus is increased in strength, the extensor contraction in the third phase of the compound reaction increases with increase in strength of the contralateral stimulus.

16. In some cases the extensor rebound of the "pure" flexion-reflex decreases in value with increase in the strength of stimulus. This may take the form of a reduction of the maintenance of the rebound—the reduction being of the nature of a sharp relaxation. When this occurs it may also be seen in the third phase of the compound reaction. The contraction phase in the third phase of the compound reaction is augmented as compared with the extensor rebound of the flexion-reflex. The relaxation phase increases with increase of the strength of ipsilateral stimulus (a reciprocal flexor contraction may even appear), and decreases with

increase of strength of the contralateral "background" stimulus. Its occurrence in the third phase of the compound reaction seems to shew that the relaxation of the extensor rebound is, as it were, due to "active inhibition."

17. In the "fourth" phase of compound reactions the phenomena where there is extensor after-discharge in the "pure" extension-reflex have already been summarised (see section 11 of this summary).

18. Where "extensor rebound relaxation after excitation" is present in the "pure" extension-reflex it may also occur in the "fourth phase" of compound reactions. If the relaxation is incomplete in the "pure" reflex it becomes greater—and sometimes complete—in the compound reaction. If complete in the "pure" reflex it may become accompanied by a flexor rebound contraction in the compound one—although that is absent in the "pure" contralateral reaction.

19. If the temporal relations of stimuli of constant strength are varied in a series of compound reactions in which this phenomenon occurs, it is found that the extensor terminal relaxation becomes greater the later the ipsilateral stimulus falls in the period of the extension "background" (that is, also, the shorter the period of the third phase—or the shorter the interval which separates the fourth phase from the phase of double stimulation). Where reciprocal flexor rebound contraction appears, that also becomes greater under these conditions.

20. Where the strengths of the stimuli are varied it is found that the extensor terminal relaxation—and the flexor rebound contraction if that appears—are greater the stronger the ipsilateral flexion-producing stimulus is.

21. Where "flexor rebound contraction after inhibition" accompanies "extensor rebound relaxation after excitation" in the "pure" contralateral extension-reflex, the fourth phase of the compound reaction in which extension is the "background" is almost invariably characterised by an increase in the flexor rebound contraction. This increase is augmented pari passu with augmentation of the strength of the interrupting flexion-producing ipsilateral stimulus, and it seems also to be augmented when the ipsilateral stimulus is made to fall late in the period of the extension "background." These phenomena in the fourth phase seem to be conditioned chiefly by the ipsilateral interrupting stimulus; and it appears as if the influence of this, as it were, can persist over a period (the third phase of the compound reaction) in which the antagonistic activity (extension) becomes reëstablished—seemingly in full force.

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STUDIES IN THE PHYSIOLOGY OF THE NERVOUS SYSTEM. XVII.: DECEREBRATE PREPARATIONS, SUCCESSIVE PHENOMENA IN COMPOUND REACTIONS—STIMULI OF ASYNCHRONOUS TERMINATION WHERE THE FLEXION-REFLEX IS LEFT IN ACTION. By T. GRAHAM BROWN (Manchester). (With sixteen figures in the text.)

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# STUDIES IN THE PHYSIOLOGY OF THE NERVOUS SYSTEM. XVII.[1]: DECEREBRATE PREPARATIONS, SUCCESSIVE PHENOMENA IN COMPOUND REACTIONS—STIMULI OF ASYNCHRONOUS TERMINATION WHERE THE FLEXION-REFLEX IS LEFT IN ACTION.

By T. Graham Brown (Manchester).[2] (With sixteen figures in the text.)

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CONTENTS.



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[1] The preceding papers have appeared in this Journal: vol. ii, No. 3, p. 243, 1909; vol. iii., No. 1, p. 21, 1910; vol. iii., No. 2, p. 139, 1910; vol. iii., No. 3, p. 271, 1910 (in collaboration with Miss Abel); vol. iii., No. 4, p. 319, 1910; vol. iv., No. 1, p. 19, 1911; vol. iv., No. 2, p. 151, 1911; vol. iv., No. 3, p. 273, 1911; vol. iv., No. 4, p. 331, 1911; vol. v., No. 3, p. 233, 1912; vol. v., No. 3, p. 237, 1912; vol. vi., No. 1, p. 25, 1913; vol. vi., No. 3, p. 209, 1913; vol. vii., No. 3, p. 197, 1913; vol. vii., No. 3, p. 245, 1913; vol. vii., No. 4, p. 293, 1913.

[2] The expenses of this research have been defrayed by a grant from the Carnegie Trust. The work was done in the Physiology Laboratory of the University of Liverpool during the tenure of a Carnegie Fellowship.

## I. Introduction.

In the paper of this series which immediately precedes the present one the "successive" or "terminal phenomena" of compound stimulation were examined when the "background" is one of contralateral extension. In the present paper the phenomena are examined in experiments in which the ipsilateral flexion-reflex forms that "background" for the compound reaction. As before, the successive phenomena are investigated in two distinct phases of compound reactions in which the interrupting stimulus is withdrawn before the "background"—the "third phase" of the compound reaction (in which the "background" stimulus is still in action) and the "fourth phase" (which is that after the withdrawal of the "background" stimulus).

Since the preceding papers of this series were written, Beritoff[1] has published a paper in which he notices one of the successive effects of compound stimulation in the reflex reactions of the frog after local poisoning of the lumbar spinal cord with strychnine. When a "background" of flexion is used and the interrupting "Abwischreflex" is again withdrawn during the continuation of that "background," an extensor after-discharge occurs in the third phase of the reaction. This, which is present in the "pure" interrupting reflex, is accompanied by a lasting relaxation of the flexor.

## II. Methods Employed.

The methods employed in the present experiments were the same as those described in previous papers in this series. The animals (cats) were unconscious throughout each experiment from the commencement and until they were destroyed at its termination.

[1] Ar. f. (An. u.) Phys., 1913, p. 1.

## III. Successive Phenomena in Compound Stimulation: Stimuli of Asynchronous Termination — Ipsilateral Flexion-Reflex ("Background") left in Action—No Rebound Contractions present in the Simple Reflexes.

When the "background" stimulus used is the ipsilateral, and with this a contralateral stimulus is compounded, the rule in these experiments has been to apply first the ipsilateral stimulus—that is to say, to produce a flexion-reflex—and then during the period of this stimulation to commence a contralateral stimulus (extension-reflex) and to withdraw this again before the termination of the ipsilateral reaction. When this is done, the successive effects of the contralateral stimulus upon the flexion-reflex may be studied first in that phase of the compound reaction which extends from the point of cessation of the contralateral reaction to that of the ipsilateral; and secondly, in the phase which immediately succeeds the termination of the ipsilateral stimulus. Such a compound reaction may be divided into four phases. Of these the first is that of "pure" ipsilateral flexion; the second is that of double stimulation, when the two stimuli are being synchronously applied; the third is the phase of flexion complicated by the after-effects of the contralateral stimulus alone; and the fourth is the terminal phase after the withdrawal of the ipsilateral stimulus when the centres are returning to the normal state of "rest."

In this section the phenomena are examined in experiments in which the "pure" flexion-reflex is followed by flexor relaxation only, and in which the "pure" extension-reflex is followed only by a maintained extensor after-discharge.

### A. Successive Phenomena during the Continuation of the Ipsilateral Flexion-Reflex ("Background") after Double Stimulation ["Third Phase" of the Compound Reaction].

In the third phase of the reaction the ipsilateral stimulus continues uncomplicated by the presence of the contralateral. It might therefore be expected that here there occurs a restitution of the flexor contraction from the level to which, by inhibitory relaxation, it was depressed in the period of double stimulation up to the level of contraction which would have obtained had the ipsilateral stimulus remained throughout uncomplicated by a contralateral. In point of fact, such restitution is found often to occur, or at least to be attempted, in the decerebrate preparation. But, as in the low spinal preparation, there is in some cases little or no restitution. Such instances may first be examined.

In a certain number of decerebrate preparations, then, it is found that there is in the third phase little or no restitution of flexor contraction from the level of depression conditioned during double stimulation. There is little to describe. The flexor contraction is reduced during the period of double stimulation, and this reduction may continue to increase in value

for a short period after the termination of the contralateral stimulus. Thereafter the flexor curve may remain level at the lowest point attained during (or rather immediately after) double stimulation. In other cases there may be a slight increase of the level of contraction during the continued application of the ipsilateral "background" stimulus.

In the first phase of the reaction the extensor exhibits inhibitory relaxation; in the phase of double stimulation (if the contralateral stimulus is relatively strong enough) it shews a degree of contraction which is less than that of the "pure" contralateral extension-reflex evoked with the same strength of stimulus. During the third phase this contraction as a rule diminishes even when the flexor shews no restitution from the level of depression in the phase of double stimulation. The relaxation of the extensor in this phase is a comparatively slow movement—a gradual fall which may not attain its minimum at the end of two seconds. Such a result has been observed in experiments in which soleus alone is used as the extensor [see xv., fig. 13].[1] In other instances the extensor may remain in comparatively level contraction throughout the third phase. Sometimes in the course of this there may be a partial relaxation and subsequent reconstitution of the maintained extensor contraction; and this may be accompanied, in the flexor curve, by a reciprocal contraction and relaxation (fig. 1). Occasionally in the decerebrate preparation—when the ipsilateral stimulus is comparatively weak — there may be complete inhibitory relaxation of the flexor in the period of double stimulation, and absolutely no restitution of flexor contraction in the ensuing third phase. Even where this occurs there may be in the third phase a slow relaxation of the extensor from the level of contraction attained in the second phase—that of double stimulation.

In series of compounded reactions in which the time relations of the two stimuli are altered, but in which their values remain constant, the flexor depression in the third phase appears to be greater the later in the period of ipsilateral stimulation the contralateral stimulus falls.

It may be remarked that, in general, where in the third phase of the compound reaction there is continued flexor depression accompanied by continued extensor contraction, the contralateral extension-producing stimulus has usually been comparatively strong; and, moreover, it has usually been followed on cessation by a strong extensor after-discharge. In these instances the phenomena in the third phase seem to be conditioned by the compounding of immediate flexion with terminal extensor after-discharge. And the latter wins. But the occasional slight flexor restitution of contraction which is again followed by depression may be the evidence of a slight factor of flexion in the early part of the extension terminal phenomena—a factor not evidenced as such in the "pure" ex-

[1] In this paper, as in those which immediately precede it in this series, references to figures in other papers in the series are given—i.e. "[see xv. fig. 13.]" This means "see fig. 13 in paper xv. of this series."

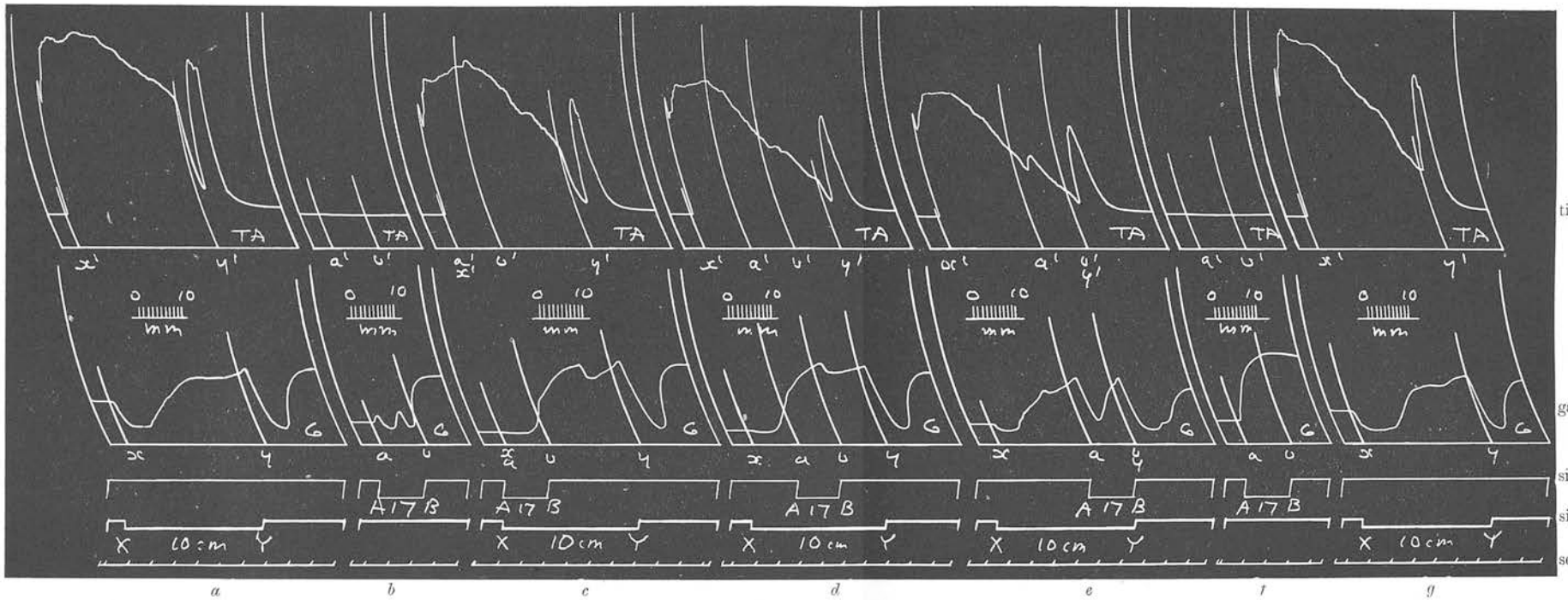


FIG. 1.—Experiment C, clxviii., record 298, 7672 ; 27/2/13.—Decerebrate cat. A series of compound reactions obtained 3 hours and 24 minutes after decerebration—minute intervals.

Reactions *a* and *g* are "pure" ipsilateral flexion-reflexes—strength and duration of stimulus the same as those in the compound reactions. Note that the flexor rebound contraction is of about the same extent before and after the series of compound reactions. The flexion-reflex is of "decerebrate" type—there being late extensor contraction during stimulation. This shews a relaxation reciprocal to the flexor rebound, and thereafter the extensor contraction is again constituted as an extensor rebound contraction of maintained type.

Reactions *b* and *f* are "pure" extension-reflexes—strength and duration of stimulus as in the compound reactions. Note that *b* is of "decerebrate" type and *f* of "spinal" type. In either case there is a maintained extensor after-discharge.

In reactions *c*, *d*, and *e* the two stimuli are compounded in different temporal arrangements. Note that the flexor rebound contraction on withdrawal of the flexion "background" is smaller the later the contralateral stimulus falls. The secondary extensor rebound also occurs later and is of less extent. The reduction of the flexor rebound is greatest in *e*, where the two compounded stimuli are synchronously withdrawn. Note in the third phase (between ordinates *b*, *b'-y*, *y'*) of reaction *d* the extensor relaxation and reciprocal flexor contraction. Thereafter the extensor contraction is reconstituted. Note, in the phase of double stimulation of reaction *e*, extensor relaxation and reciprocal flexor contraction. Thereafter extensor contraction occurs.

This figure demonstrates the reduction of flexor rebound in the flexion-reflex when compounded with an extension-reflex which exhibits extensor after-discharge.

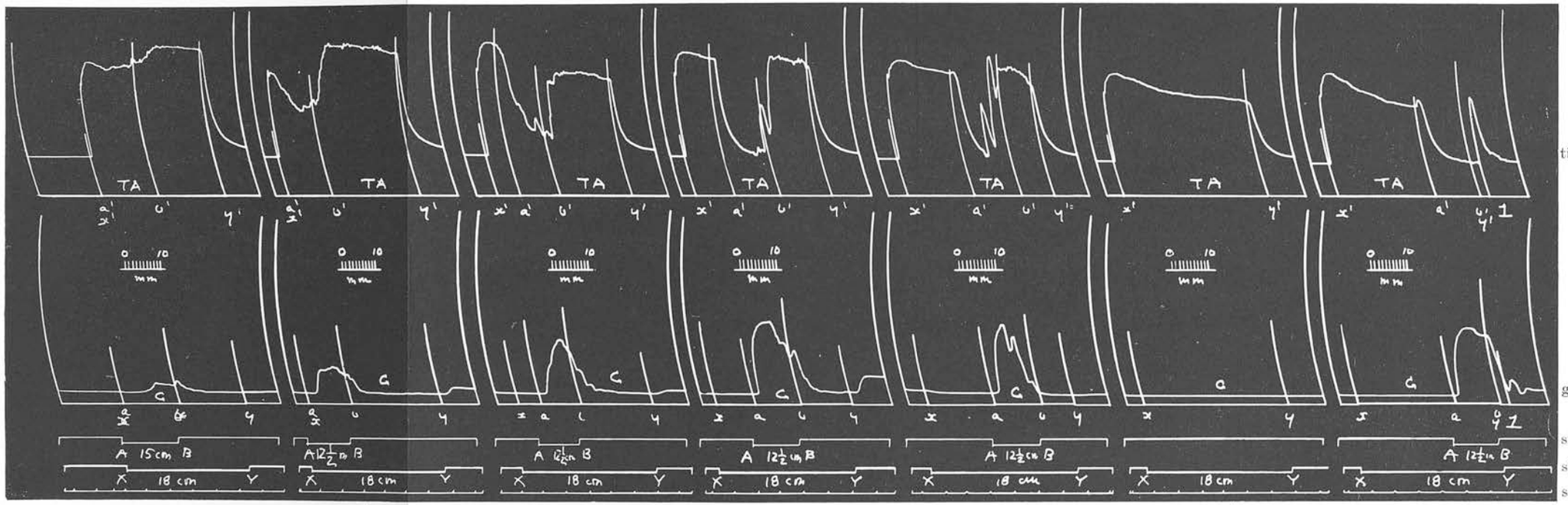


FIG. 2.—Experiment C, clxiii., record 261, 6142; 2/11/12.—Decerebrate cat. A series of compound reactions obtained 2 hours and 6 minutes after decerebration—minute intervals.

Reaction *f* is a "pure" flexion-reflex—strength and duration of stimulus as in the compound reactions. Note that throughout the series there is a deterioration of the value of the flexion-reflex. Note also that there is no rebound contraction on cessation of stimulation—only flexor terminal relaxation.

No instance of the "pure" extension-reflex is reproduced. Its extent was slightly greater than that of the extensor contraction in the first phase of reaction *e* of fig. 8 in the immediately preceding paper of this series (xvi.). The reactions of that figure were immediately precedent to the present one in time. On cessation of a 2-second contralateral stimulus there was a sharp extensor relaxation (extensor terminal relaxation—"rebound relaxation after excitation") which was partial and left a slight and rapidly waning extensor after-discharge.

In reaction *a* the strength of contralateral stimulation is weaker than in the other compound reactions of the series. Compare it with *b* to demonstrate the slighter flexor relaxation and the slighter extensor contraction during the phase of double stimulation.

In reactions *b*–*e* and *g* the contralateral stimulus is applied ever later in the period of the flexion-reflex. Note that during double stimulation there is, upon the whole, a greater flexor relaxation and extensor contraction the later the contralateral stimulus falls. In *e* there is a rhythmic phenomenon during double stimulation. In the third phases of the compound reactions the flexor restitution is complete, and extensor relaxation occurs. In *g* the two stimuli are synchronously withdrawn. There occurs a marked flexor rebound contraction which is present in neither "pure" reflex. In this reaction observe the slight "spike-like" flexor augmentation of contraction at the commencement of the phase of double stimulation. In *b*, *c*, and *d* there is a slight extensor rebound contraction in the fourth phase of the compound reactions.

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tension-reflex, but activated, as it were, when the extension terminal phenomena are compounded against a flexion "background."

In the decerebrate preparation, however, there usually occurs in the third phase of the compounded reaction a restitution of flexor contraction which is either partial or complete—while sometimes there may even be augmentation of the flexor contraction above the level which would have obtained had the ipsilateral stimulus been uncomplicated.

Where the restitution of flexor contraction is partial or complete little need be said. During the period of double stimulation the flexor contraction is more or less depressed as the contralateral stimulus is stronger or weaker. This depression persists for a short period after the cessation of the contralateral stimulus and then gives place to a state of increasing contraction which forms the flexor restitution (figs. 2, 6). There is sometimes an increase of the flexor depression immediately on withdrawal of the contralateral stimulus—perhaps corresponding to a "flexor rebound relaxation after inhibition." The flexor restitution is usually a sudden movement which at once carries the level of contraction up to (or nearly to) the level which would have been present if there had been no interrupting contralateral stimulus. There it persists until the end of the period of ipsilateral stimulation. Sometimes the movement is a comparatively slow one, and this has been observed in cases in which there was an additional depression of the flexor contraction immediately on cessation of the contralateral stimulus. The latency of the flexor contraction in restitution is commonly much greater (as measured from the point of cessation of the contralateral stimulus) than is the latency of flexor contraction at the commencement of a "pure" ipsilateral flexion-reflex—for instance, 0·4 second in place of 0·1 second (fig. 2); 1·0 second in place of 0·1 second (fig. 6).

If, during the period of double stimulation, there is a contraction of the extensor muscle, this disappears again in the third phase of the reaction in all those cases in which there is a restitution of the flexor contraction, partial or complete. The movement of extensor relaxation as demonstrated in the curves is usually a fairly rapid one. Its latency is usually much shorter than that of the reciprocal movement of flexor contraction—for instance, 0·2 second as compared with 0·4 second, 0·5 second as compared with 1·0 second—although the relaxation of the extensor sometimes does not reach its minimum before the flexor contraction reaches its maximum.

In consecutive series of reactions the time relations of the two stimuli have been changed while their values have been kept constant.

When the time relations alone were changed (fig. 2) the restitution of flexor contraction appeared to be less the later in the period of ipsilateral stimulation the contralateral stimulus was applied (the flexor depression during double stimulation was then greater the later the contralateral stimulus was given) (see also fig. 6).

In these experiments actual augmentation of the flexor restitution has occurred in the third phase of compounded reactions. That is to say, that the level of the flexor contraction attained in restitution has been higher (and sometimes markedly higher) than the level of flexor contraction which occurred in the "pure" flexion-reflex after the same duration of an ipsilateral stimulus of strength equal to that used in the compounded reaction.

This may occur when the "pure" contralateral extension-reflex is followed by a flexor rebound contraction on cessation of stimulation, and such cases will be considered later. In experiments in which there is no flexor rebound contraction in the extension-reflex it may also occur. When this is the case it is found both in those instances in which there is flexor inhibitory relaxation in the phase of double stimulation, and in those in which there is the more rare flexor augmentation.

Where the flexor augmentation occurs after inhibitory relaxation there may be no rebound phenomena in either the flexion-reflex or the extension-reflex (figs. 3, 4, 5). The phenomenon may, however, occur when there is a flexor rebound after the flexion-reflex, and also when there are flexor rebounds after the flexion-reflex and the extension-reflex; these cases will be considered later.

The phenomenon differs from that of the ordinary restitution of flexor contraction in the third phase only in extent. The level of flexor contraction may be two or three times as high as that of the "pure" flexion-reflex, when that is not very great (fig. 3). The movement is sometimes a comparatively slow one, although often fast; and the extensor exhibits complete reciprocal relaxation.

In those instances in which there is an augmentation of flexor contraction during the phase of double stimulation there sometimes appears an additional augmentation on cessation of the contralateral stimulus even when there are no rebound phenomena in the "pure" reactions (figs. 4, 5) [see also xv., fig. 10]. In the cases in which the flexor augmentation during double stimulation attains a maximum at which it remains during the rest of the period of double stimulation, the withdrawal of the contralateral stimulus may be followed by no flexor augmentation, but only by a sustentation of the level of contraction thus reached [see xv., fig. 10]. But sometimes in this phenomenon of flexor augmentation during double stimulation there is a sharp flexor contraction succeeded by flexor relaxation which, however, brings the level of flexor contraction down to that which obtained immediately before the commencement of contralateral stimulation only. When this is the case the withdrawal of the contralateral stimulus may be followed by another augmentation which sometimes resembles that of the phase of double stimulation in again dying during the remaining portion of the period of ipsilateral stimulation. In other cases the augmentation during the third phase may be well sustained.

When the strengths of the compounded stimuli are varied in series of

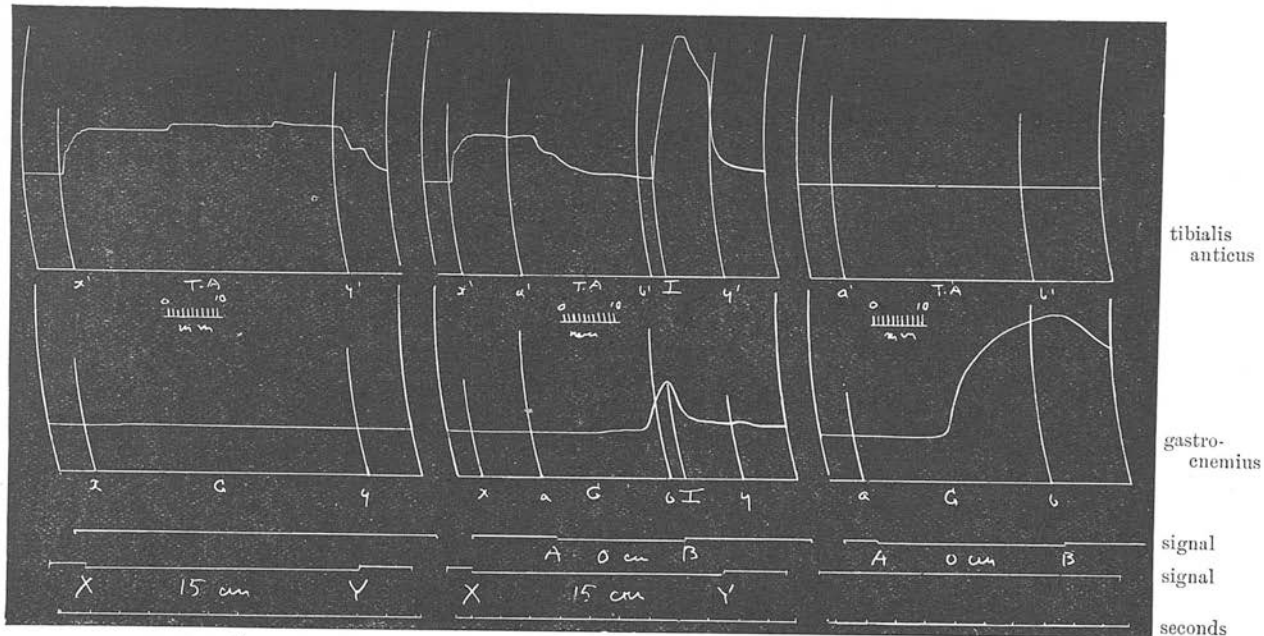


FIG. 3.—Experiment C, xxiv., record 42, 989; 14/3/11.—Decerebrate cat. Three reactions obtained 4 hours and 3 minutes after decerebration—the intervals between the reactions are 2 minutes and 4 minutes.

Reaction *a* is a "pure" flexion-reflex.

Reaction *c* is a "pure" contralateral extension-reflex—note the slight extensor terminal relaxation and the good extensor after-discharge.

In reaction *b* the two are compounded. In the phase of double stimulation there is flexor relaxation and a late extensor contraction. In the third phase there is a great augmentation of flexor contraction—so that it reaches a level of contraction far above that which obtains at the same point in the "pure" flexion-reflex.

reactions it is found that the flexor augmentation in the third phase increases in value with increase in the strength of the interrupting contralateral stimulus when the ipsilateral "background" stimulus is of constant strength (fig. 4). It must here be remembered that flexor rebound contraction may make its appearance in the "pure" extension-reflex when the strength of the contralateral stimulus is increased. Thus in one case a certain strength of contralateral stimulation gave a very weak extension-reflex which was followed by a maintained extensor after-discharge. On this being compounded against a strong flexion "background" there was flexor augmentation during double stimulation, followed by a maintenance of this in the third phase. A stronger contralateral stimulus was followed on cessation by flexor rebound; and it opened during stimulation with a transient flexion [see xi., fig. 36]. In a compound reaction of the same strength of flexion "background" there was, in the phase of double stimulation, a flexor augmentation of contraction greater in extent —as measured from the level of flexor contraction in the "pure" flexion-reflex—than that of the flexion factor in the "pure" contralateral reaction. This died during the course of double stimulation, and in the third phase of the compound reaction there was a flexor augmentation of greater extent than that of the flexor rebound contraction of the "pure" contralateral reaction. It looks here as if the presence of a flexion "background" may bring to light a latent flexion factor in the extension-reflex or in its terminal phenomena, and as if it might augment these factors if they are apparent in the "pure" contralateral reaction. In another experiment—where also there was a slight factor of flexion in contralateral reactions evoked with strong stimuli—there occurred flexor augmentation during the phase of double stimulation in compound reactions. At the same time there was an additional augmentation in the third phases of these reactions (fig. 4). These phenomena were seen when the "pure" contralateral stimulus was weak, and evoked a reaction of extensor contraction alone, followed by a "tonic" extensor after-discharge. They seemed to be greater the stronger the interrupting contralateral stimulus. Stronger contralateral stimuli were followed, on cessation of stimulation, by an incomplete extensor relaxation, after which the after-discharge was again constituted. Throughout this series the extent of the flexor augmentation in the third phases of the compound reactions was greater the stronger the interrupting contralateral stimulus. With the stronger contralateral stimuli there appeared, at the commencement of the third phases of the compound reactions, a slight flexor relaxation. This was brief, and immediately preceded the flexor augmentation of the third phase. It did not appear when the interrupting contralateral stimuli were weak. Later in this experiment (fig. 5), in a series of compound reactions, the interrupting contralateral stimulus was kept of constant strength and the value of the ipsilateral "background" stimulus was progressively increased in strength. Here this element of flexor relaxation in the early part of the third phase

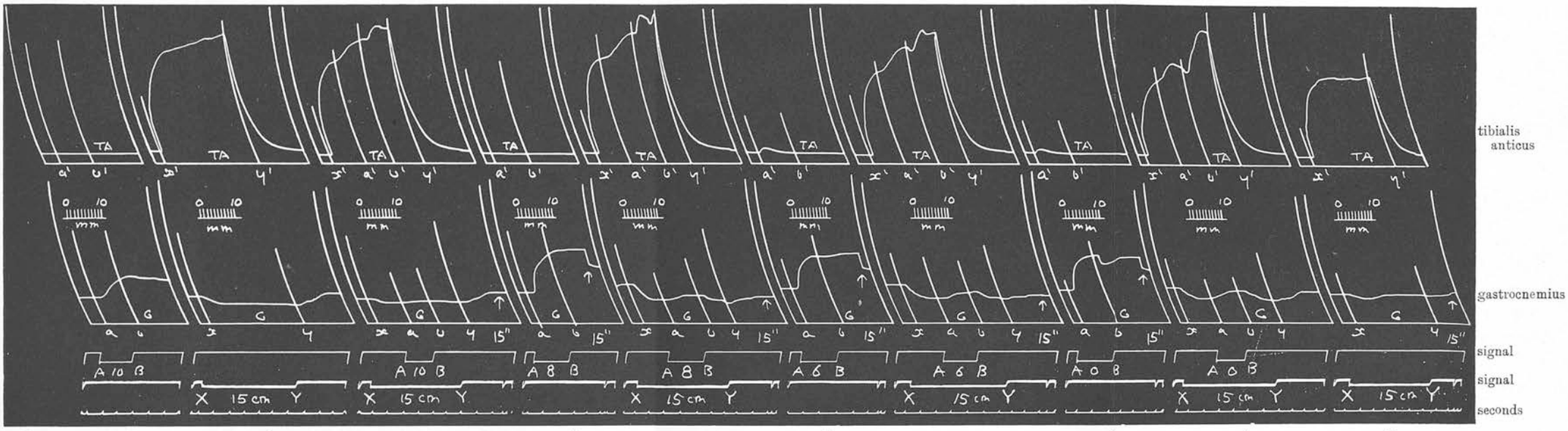


FIG. 4.—Experiment C, clxvi., record 295, 7479; 24/2/13.—Decerebrate cat. A series of compound reactions obtained 2 hours and 46 minutes after decerebration—minute intervals.

Reactions *b* and *k* are "pure" flexion-reflexes—strength and duration of stimulation as in the compound reactions. Note that deterioration of the value of the flexion-reflex occurs throughout the series. There is a slight extensor rebound contraction.

Reactions *a*, *d*, *f*, *h* are "pure" extension-reflexes taken with different strengths but with the same durations of stimulus. These strengths are the same as those used in the immediately following compound reactions in each case. Note that in this series of "pure" extension-reflexes there appears a flexor contraction at the commencement of the period of stimulation with increase in the strength of stimulus, and that there also appears an element of extensor relaxation in the extensor after-discharge.

Reactions *c*, *e*, *g*, *i* are compound—constant "background" flexion-reflex and increased strength of interrupting contralateral stimulation. During double stimulation there is flexor augmentation of contraction which is relatively greater the stronger the contralateral stimulus. In the third phases of the compound reactions there is an additional flexor augmentation which also is relatively greater the stronger the contralateral stimulus.

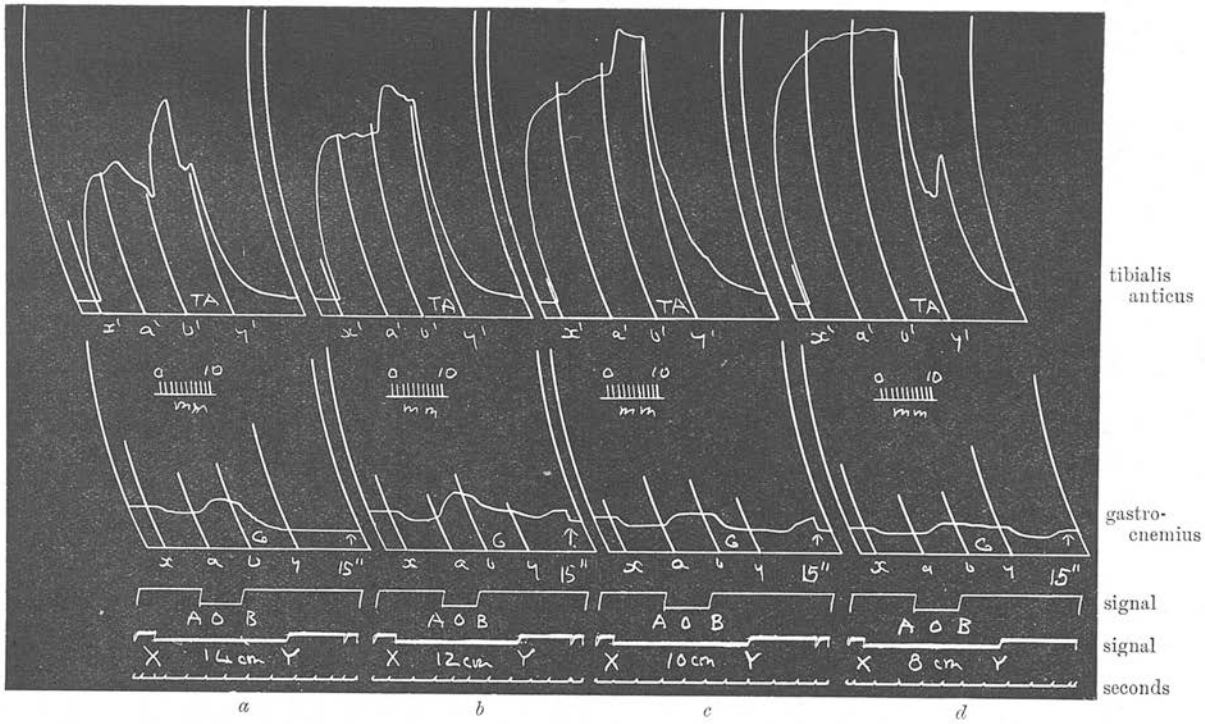


FIG. 5.—Experiment C, clxvi., record 295, 7490 ; 24/2/13.—Decerebrate cat. A series of compound reactions obtained 2 hours and 58 minutes after decerebration—minute intervals.

This series follows that of the preceding figure. Here the ipsilateral flexion "background" is progressively increased in strength. The interrupting contralateral reflex is the same in value as that registered in reaction *h* of the preceding figure.

Here there is again flexor augmentation during double stimulation, but it appears to be relatively less the stronger the flexion "background." Again, there is an additional flexor augmentation in the third phase. This also appears to be relatively less the stronger the flexion "background." Note that in reaction *a* there is a slight flexor relaxation at the commencement of the third phase. This is not seen in the remaining reactions of the series.

appeared only with weak ipsilateral flexion "background." The following flexor augmentation of the third phase—as measured from the level of the flexor contraction of the "pure" flexion-reflex—appeared to be decreased with increase in the value of the flexion "background." The flexion augmentation during double stimulation appeared also to be relatively less the stronger the "background." With strong "backgrounds" there was even relaxation in the second phase. The interrupting contralateral stimulus used evoked an extension-reflex which was complicated by a slight flexion element and followed by slight extensor relaxation.

### B. Successive Phenomena after the Discontinuation of the Ipsilateral Flexion-Reflex ["Fourth Phase" of the Compound Reaction].

On cessation of the ipsilateral stimulus there occurs the usual flexor relaxation in those cases in which no rebound phenomena are present. This has not been noticed materially to differ from the phenomenon of flexor relaxation in the "pure" ipsilateral flexion-reflex.

### IV. Successive Phenomena in Compound Stimulation: Stimuli of Asynchronous Termination — Ipsilateral Flexion-Reflex ("Background") left in Action — Rebound Contractions present in the Simple Reflexes.

When rebound phenomena are present in the "pure" reflexes they may be classified as being in the direction either of extension or of flexion both in the flexion-reflex and in the extension-reflex. The extension-reflex may be followed on cessation of stimulation either by a flexor rebound contraction accompanied by reciprocal extensor relaxation (or by the extensor relaxation alone), or by an extensor rebound after excitation—which perhaps is but an exaggeration of the more ordinary tonic extensor after-discharge. The flexion-reflex is followed in some cases by a flexor rebound contraction (and sometimes by an extensor relaxation after inhibition), but more commonly by an extensor rebound contraction. The extensor rebound, either after inhibition in the flexion-reflex or after excitation as the tonic after-discharge of the extension-reflex, is the most common terminal phenomenon of the reflexes which occur in the antagonists of the ankle-joint. According as these rebound phenomena vary in the "pure" reactions we may examine the successive phenomena in their compound reactions; and, as before, we may investigate the successive effects of the compounded stimuli either in the third phase of the compound reaction (that which commences when the contralateral stimulus is withdrawn, and lasts as long as the ipsilateral "background" stimulus is continued) or in the fourth phase (which is that after cessation of all stimulation), in which the centres again pass into the state of "rest."

## A. Successive Phenomena during the Continuation of the Ipsilateral Flexion-Reflex ("Background") after the Period of Double Stimulation [Third Phase of the Compound Reaction].

We may first examine the cases in which the terminal phenomena of the "pure" reflexes are predominantly in the direction of extension—the extensor rebound contraction after cessation of the ipsilateral flexion-reflex, and the tonic extensor after-discharge or the extensor augmentation of contraction ("extensor rebound contraction after excitation") after cessation of the contralateral extension-reflex.

### 1. Where "Extensor Rebound Contraction after Excitation" is present in the "Pure" Extension-Reflex.

When there is an extensor augmentation on cessation of stimulation in the "pure" contralateral extension-reflex it may happen that with a strength of stimulus which is insufficient to evoke any contraction of the extensor during stimulation there may yet be an extensor rebound contraction on withdrawal of the stimulus. In one experiment in which this occurred there was also an extensor rebound contraction after the ipsilateral flexion-reflex. On compounding the two it was found that withdrawal of the ineffective contralateral stimulus while the ipsilateral was still in being was yet followed by a well-marked extensor contraction which in every way was similar to the extensor rebound of the ineffective "pure" contralateral stimulus (fig. 13, reaction *a*). In such a case restitution of flexor contraction is proportionately depressed or delayed. Where the contralateral stimulus is not only effective in giving an extensor contraction in the "pure" reflex but also gives an extensor contraction when applied during the flexion-reflex, this may not disappear again in the third phase after withdrawal of the contralateral stimulus. In such cases the extensor slowly relaxes during the third phase of the compounded reaction, and there is flexor depression in this phase. There may occur no restitution of flexor contraction during the two final seconds in which the ipsilateral stimulus continues uncomplicated by the contralateral. This has been observed to occur when the "pure" contralateral reflex was followed on cessation of stimulation by a sustained tonic extensor after-discharge, and when the ipsilateral flexion-reflex on cessation was followed by a well-marked extensor rebound contraction which was also maintained after its establishment [see xv., fig. 13]. Where, in the "pure" contralateral extension-reflex, there is an "extensor rebound contraction after excitation"; and when, in the phase of double stimulation, extensor contraction and flexor relaxation occurs, the commencement of the third phase may be marked by an augmentation of extensor contraction. This is, however, much smaller in extent than in the "pure" extension-reflex. Accompanying this there is a reciprocal augmenta-

tion of the flexor relaxation which occurs in the phase of double stimulation. Thereafter the flexor contracts and the extensor relaxes. In a series of reactions in which the time relations of the two stimuli were varied it was found that the reciprocal phenomena of extensor augmentation of contraction and flexor augmentation of relaxation were slightly greater the later in the period of ipsilateral stimulation the contralateral stimulus was applied. In the final reaction of the series the contralateral stimulus was applied late in the period of ipsilateral stimulation (four seconds after its commencement) and the two stimuli were simultaneously withdrawn. There ensued a very large augmentation of the extensor contraction which had appeared during the phase of double stimulation. This was much greater than in the "pure" contralateral extension-reflex. At this period in the experiment, and with the strength of ipsilateral stimulation then used, there was no extensor rebound contraction after the flexion-reflex (fig. 6). On cessation of the ipsilateral "background" stimulus (when the two stimuli were terminated asynchronously) there was an extensor rebound contraction which was greater the later the contralateral stimulus fell in the period of the ipsilateral "background" stimulus, and the shorter the period of the third phase.

### 2. Where "Extensor Rebound Relaxation after Excitation" is present in the "Pure" Extension-Reflex.

Having already discussed those cases in which there is the usual extensor after-discharge in the "pure" extension-reflex, we may now look at the cases in which there is a terminal relaxation of the extensor muscle in that reflex.

Above have been described cases in which the weak extension-reflex was followed by extensor after-discharge, but in which increased strengths of contralateral stimulation evoked extension reactions which were followed by terminal extensor relaxation (fig. 4). There was augmentation of flexion in the third phase of compound reactions in which these contralateral stimuli were used as the interruptors.

Where the extensor relaxation after the "pure" contralateral extension-reflex is of very slight extent there may be no augmentation of flexion in the third phase of the reaction in which it is compounded against a flexion "background." If the flexion is weak and the extension strong there may even be a more or less complete depression of flexion in that phase [see xv., fig. 13]. The extensor contraction may then shew persistence in the third phase—but this is of less extent than is the partial extensor after-discharge of the "pure" extension-reflex. Even where there is a considerable extensor terminal relaxation in the "pure" extension-reflex there may yet, in the third phase of the compound reaction, be only complete restitution of flexor contraction, and no augmentation (or very slight augmentation) of it above the level which obtains in the "pure" flexion-reflex (fig. 2). But

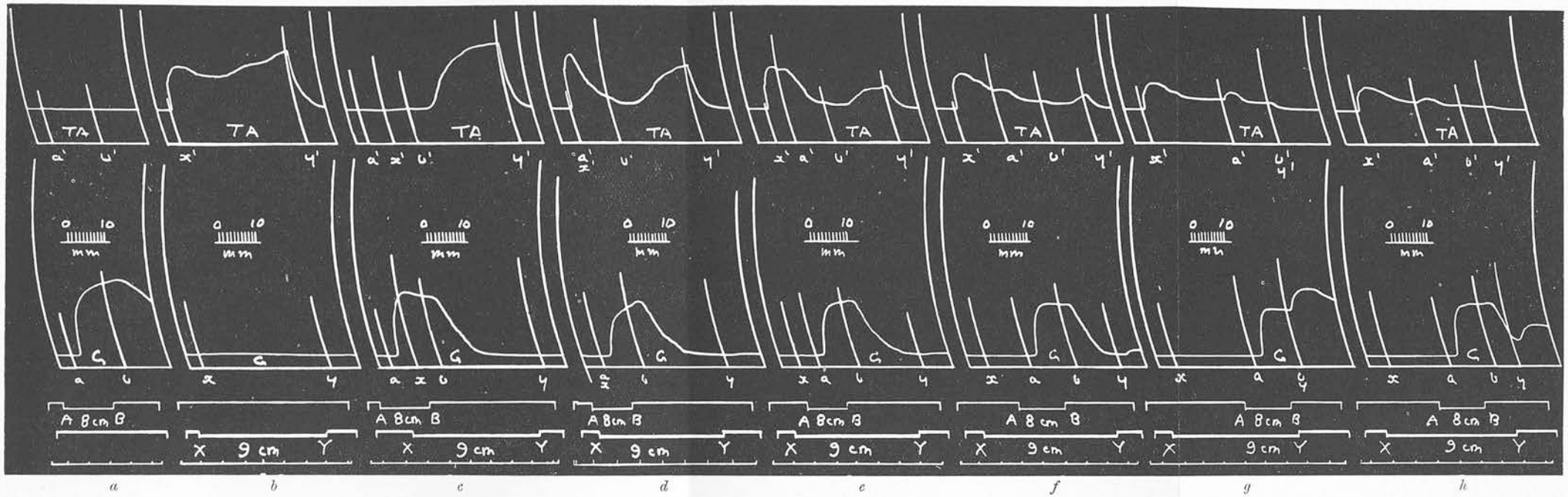


FIG. 6.—Experiment C, cxliv., record 262, 6187 ; 3/12/12.—Decerebrate cat. A series of compound reactions obtained 2 hours and 47 minutes after decerebration—minute intervals.

Reaction *a* is a "pure" extension-reflex—strength and duration of stimulation the same as those used in the compound reactions. There is a slight augmentation of extensor contraction on cessation of stimulation, and this is followed by a slow extensor relaxation. There was a much better marked "extensor rebound contraction after excitation" earlier in the experiment.

Reaction *b* is a "pure" flexion-reflex—strength and duration of stimulation those used in the compound reactions. Note the peculiar form of the flexor contraction, the absence of any rebound contraction, and the fact that a certain deterioration of the value of the flexion-reflex occurs in the series of compound reactions.

Reactions *c–h* are compound, and the temporal relations of the two stimuli are varied. In *c* the contralateral stimulus is first applied and first withdrawn—double stimulation lasting 1 second only. In *d* the two stimuli are commenced synchronously and double stimulation is for a period of 2 seconds—as it is in the remaining compound reactions. In *e* double stimulation commences 1 second after the commencement of the "background" flexion-reflex ; in *f*, 2 seconds; in *g*, 4 seconds (the two stimuli being synchronously terminated); and in *h*, 3 seconds.

Note that in *c–h* there is flexor augmentation in the first part of the period of double stimulation. This appears to be rather better marked (as measured from the level of flexor contraction in the flexion-reflex) the later the contralateral stimulus falls. The curve of extensor contraction during double stimulation appears to be rather greater in extent as well as a sharper movement the later the contralateral stimulus falls—although at the same time its latency appears also to be slightly greater.

In the third phase of the compound reactions (ordinates *b*, *b'–y*, *y'*) there appears first to be a slight augmentation of extensor contraction. This is less than that of the "pure" extension-reflex, but appears to be greater the later the contralateral stimulus falls in the period of the ipsilateral. It is accompanied by a very slight increase in flexor relaxation. In the later members of the series there appears to be a persisting flexor depression in the third phase.

In the fourth phases of the compound reactions (after ordinates *y*, *y'*) there is extensor rebound contraction in the later members of the series. This is not present in the "pure" flexion-reflex (*b*) ; absent also in *c* ; present, but very slight, in *d* and *e* ; better marked in *f* ; still better marked in *h*. In *g*—where the two stimuli are synchronously terminated—there is a very marked extensor rebound which appears as a direct augmentation of the extensor contraction of double stimulation. This may be regarded as a marked augmentation of an "extensor rebound contraction after excitation." This series therefore demonstrates, amongst other things, the appearance of an extensor rebound contraction after the flexion-reflex when that is compounded with an interrupting extension-reflex which has a comparatively well-marked extensor after-discharge. And it demonstrates that this is better marked the later the contralateral extension-producing stimulus falls in the period of the flexion-reflex.

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more usually actual augmentation of flexion occurs in the third phase of the compound reaction. This is especially the case in those experiments in which the contralateral reflex is one in which there is an element of flexion, or in which the "decerebrate" type is presented. In such cases there is often flexor augmentation in the first part of the phase of double stimulation in the compound reactions. This in part may disappear, but there then occurs a second augmentation of flexion on withdrawal of the contralateral stimulus—even when that withdrawal in the "pure" contralateral reaction is followed by extensor relaxation alone and by no flexor terminal contraction.

In one experiment the strength of ipsilateral stimulation used was subliminal. The "pure" contralateral extension-reflex was followed by complete extensor terminal relaxation, but not by a flexor rebound contraction. In the compound reactions a flexor rebound occurred in the third phase immediately on withdrawal of the contralateral stimulus. Here, as it were, the subliminal flexion "background" summated with a flexor rebound which was dormant in the "pure" extension-reflex and brought it into being.

Where, in series of compound reactions, the temporal relations of the antagonistic stimuli are varied, the flexor augmentation in the third phases may also vary (fig. 15). In one such case the flexor relaxation during double stimulation was greater the later the interrupting contralateral stimulus fell in the period of the ipsilateral "background" stimulus. At the same time there occurred flexor augmentation in the third phases, and this was found also t be greater. In the phase of double stimulation there occurred extensor contraction which was not as great as that of the "pure" extension-reflex. The later contralateral stimulation fell in the compound reactions the greater was the extensor contraction during double-stimulation, and the sharper was the extensor relaxation which occurred in the third phase.

In several instances the strengths of the compounded stimuli have been varied in series of reactions. Where the "pure" flexion-reflex is of markedly "decerebrate" type—with a great preponderance of extension—there may occur extensor augmentation during double stimulation [see xv. fig. 26]. The withdrawal of the contralateral stimulus may then be followed by partial extensor relaxation. If there is incomplete terminal relaxation of the extensor in the "pure" extension-reflex there may appear to be, in the third phase of the compound reaction, a summation of the reduced extensor after-discharge in the extension-reflex and of the extensor contraction in the flexion-reflex. In such a case, where the ipsilateral "background" is kept constant, the extensor relaxation of the third phase may appear to be greater the stronger the contralateral stimulus. In an experiment in which this was recorded three successive series of reactions were registered. In these, three different strengths of ipsilateral "background" were used; and in each series the same four different strengths of

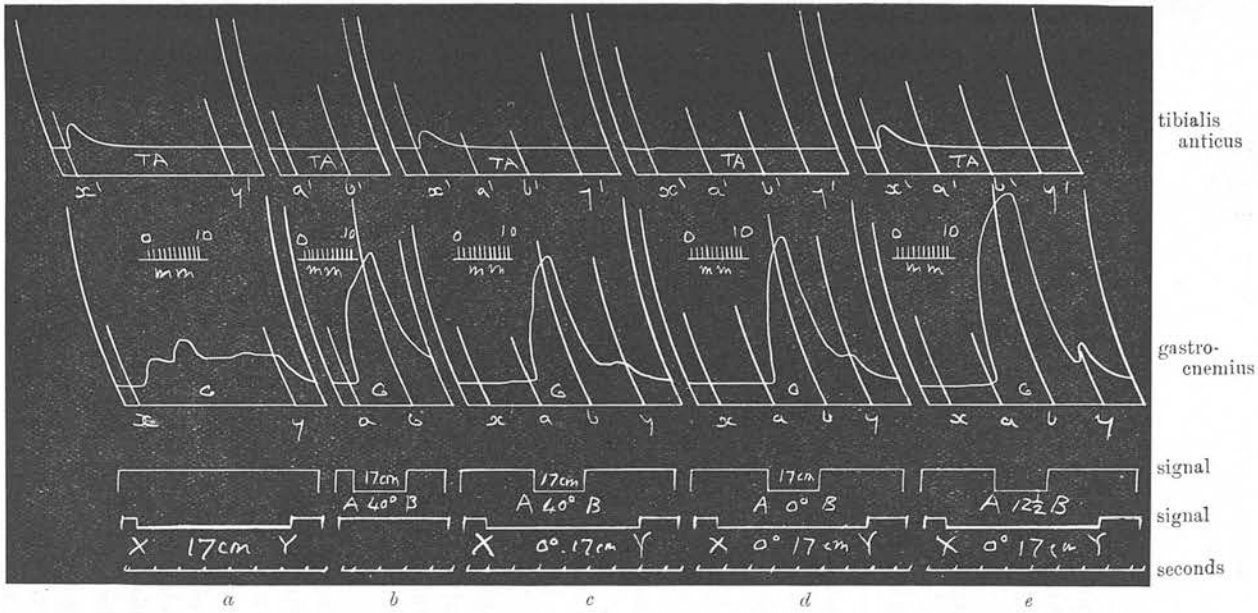


FIG. 7.—Experiment C, clxix., record 301, 7826; 28/2/13.—Decerebrate cat. A series of compound reactions obtained 4 hours and 43 minutes after decerebration—minute intervals. In this and the following three figures the reactions form a series, there being minute intervals between them. The series is composed of three sets of compound reactions in which there are used three different strengths of "background" ipsilateral flexion-producing stimuli. In each set the same three strengths of contralateral interrupting extension-producing stimuli are used. The fourth figure of the series (fig. 10) is a repetition of the last combination in the third figure (fig. 9).

Reaction *a* is a "pure" flexion-reflex—strength and duration of stimulus the same as those used for the "background" in the compound reactions of this figure. Note the slight primary element of flexion and the late extensor contraction. This is irregular, and the whole reaction is markedly of "decerebrate" type.

Reaction *b* is a "pure" extension-reflex of the value of stimulation used in reaction *c*. On comparison with reactions *g* and *m* in the succeeding figures it will be noticed that a certain deterioration of the value of the extension-reflex at this strength of stimulus occurs throughout the series. The "pure" extension-reflex of the greatest value used in this series (in reaction *e*) was of such extent that the curve nearly touched the abscissa of the flexor muscle record (see reaction in *q* in fig. 10).

Note the absence of terminal phenomena (save extensor relaxation) in the "pure" flexion-reflex, and the presence of extensor terminal relaxation in the "pure" extension-reflex.

Reactions *c*, *d*, and *e* are compound, the strength of the contralateral interrupting stimulus being progressively increased. The extensor contraction in the phase of double stimulation progressively increases with increase in the strength of the contralateral stimulus, but it is never as great as in the corresponding "pure" extension-reflex. In the third phases there occurs extensor relaxation. This commences later the stronger the contralateral stimulus is. Having reached a maximum of relaxation there is a slight restitution of extensor contraction. In *e* this looks like a small extensor rebound contraction, but it commences before the withdrawal of the ipsilateral "background" stimulus. Compare the phenomena in the third phase with the corresponding phenomena in the two following figures. In the fourth phases there is only extensor relaxation.

It should be observed that in the "pure" extension-reflex (*b*, see also *q*, fig. 10) this restitution of extensor contraction does not occur in the 2 seconds of terminal phenomena registered. Further, it should be noticed that there appears to be a certain deterioration of the extension factor of the ipsilateral "background" during the series—at any rate as estimated from the appearance of the 2 seconds of the first phases (ordinates $x$, $x'$–$a$, $a'$), where the "background" is "pure." It appears as if in the third phases of the compound reactions there is a certain summation of the extension factor of the flexion-reflex and that of the terminal phenomena in the extension-reflex.

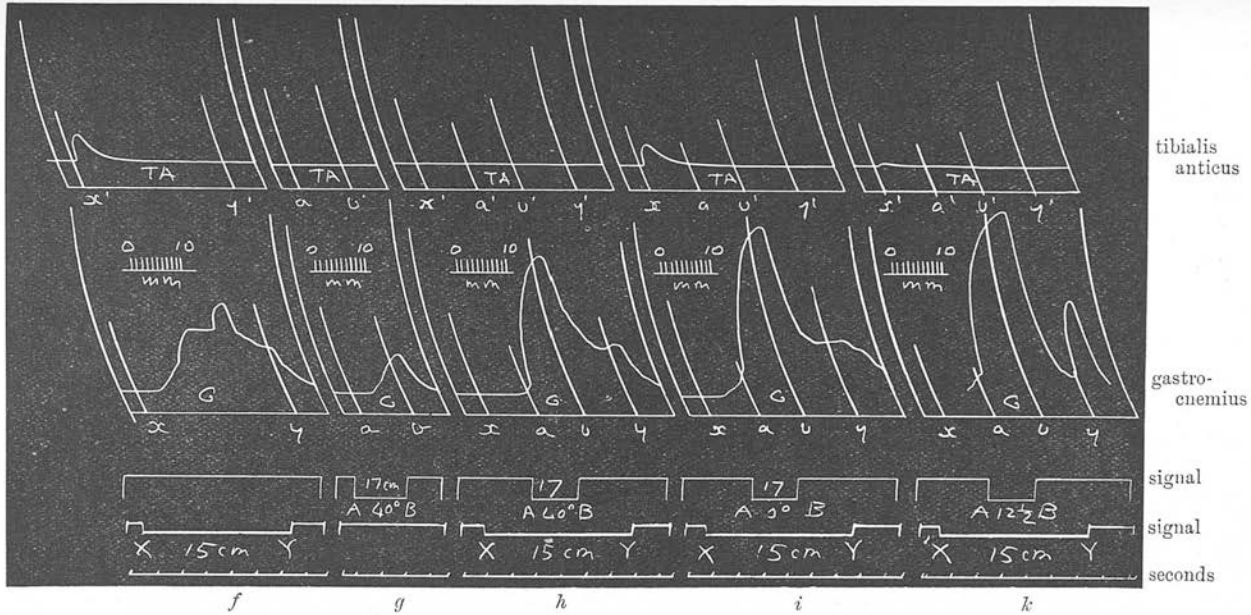


FIG. 8.—Experiment C, clxix., record 301, 7831; 28/2/13.—Decerebrate cat. A series of compound reactions obtained 4 hours and 48 minutes after decerebration—minute intervals. With figs. 7 and 9 this forms a series of three sets of compound reactions.

Reaction *f* is a "pure" flexion-reflex—same strength and duration of stimulus as in the compound reactions. The strength is greater than in the previous figure—note the greater extent of the extension element.

Reaction *g* is a "pure" extension-reflex of the strength of stimulus used in reaction *h*.

Reactions *h*, *i*, and *k* are compound. The same three strengths of contralateral stimuli used in the preceding figure are used here. In the phase of double stimulation there is in *h* a greater extent of extensor contraction than in the corresponding "pure" extension-reflex—in fact, a summation and an augmentation of the extension factors in the ipsilateral and contralateral reactions. In *k* it is less, and less also than is the extensor contraction in the corresponding reaction (*e*) of the previous figure (where the "background" is weaker). In the third phases of the compound reactions there is extensor relaxation. In *h* and *i* this is less complete than in the corresponding reactions of the previous figure (*c* and *d*). There is also extensor restitution here late in the period of the third phase. In *k* the extensor relaxation is of about the same extent as in *e*. It is followed in the fourth phase by a marked extensor rebound contraction.

It looks here as if in the third phases there was a summation of the extensor contractions of the extension factors in the flexion-reflex and in the terminal phenomena of the extension-reflex. If this is the case it will account for the greater extent of the extension elements in the third phases of *h* and *i* as compared with that in *c* and *d* (fig. 7); whereas the smaller extent of it in *k* (relatively to that in *h* and *i*) may be explained on the assumption that the extensor terminal relaxation in the "pure" extension-reflex increases in value with increase in the value of the exciting stimulus. The extensor rebound contraction in the fourth phase of that reaction is a phenomenon of some peculiarity.

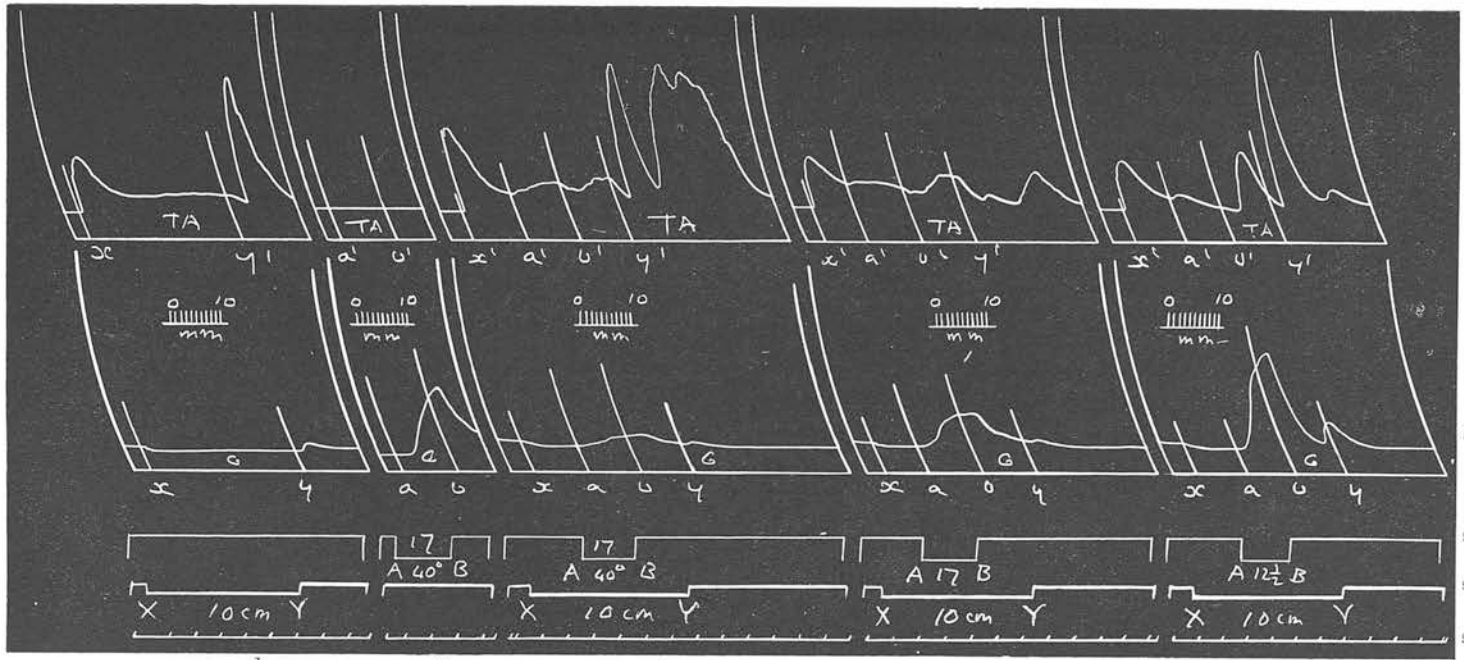


FIG. 9.—Experiment C, clxix., record 301, 7836; 28/2/13.—Decerebrate cat. A series of compound reactions obtained 4 hours and 53 minutes after decerebration—minute intervals. This figure is a direct continuation of figs. 7 and 8. The "background" used is a stronger one than that used in "8."

Reaction *l* is the "background" flexion-reflex. It will be observed that the extension element during stimulation has disappeared. On cessation of stimulation there is first a slight extensor rebound contraction, and this is followed by a well-marked flexor rebound contraction.

Reaction *m* is a "pure" extension-reflex of the value of contralateral stimulation used in the compound reaction *n*.

Reactions *n*, *o*, and *p* are compound, and the strength of the flexion "background" is greater than in the previous figures. In the phases of double stimulation in the compound reactions there is a less extensor contraction than before, but it is greater the stronger the contralateral stimulus is. In *p* there is a slight preliminary flexor augmentation in this phase.

In the third phases extensor relaxation occurs and, especially in *p*, there is an accompanying flexor augmentation. This is not maintained throughout the remainder of the phase, but gives place to relaxation before the withdrawal of the ipsilateral "background" stimulus. There is then a reciprocal extensor restitution of contraction.

In the fourth phases of *n* and *p* there is a flexor rebound contraction which is markedly greater than in the "pure" flexion-reflex. In *o* it is less. Note in *n* the curious secondary flexor rebound. In *n* and *o* there is indication of a slight preliminary extensor rebound contraction.

It looks here as if there was, as regards the extensor, algebraic summation of the inhibitory relaxation of the flexion-reflex and the terminal phenomena of the extension-reflex, in the third phase of the compound reaction. Where, in *p*, the contralateral stimulus is strongest the flexor augmentation of that phase may be explained as due to the "activation" of the flexion element in the terminal phenomena of the extension-reflex when these are superposed upon a flexion "background."

The phenomena in the fourth phases are interesting. The depression of the flexor rebound phenomena in *o* is probably accidental. It is probable that that phenomenon is greater the greater the contralateral stimulus in this experiment. If that is the case it may be explained on the assumption that the flexion element in the terminal phenomena of the extension-reflex increases with increase in the strength of the evocative stimulus. Compare with the following figure, where—in view of the contradictory result of reaction *o*—reaction *p* was repeated to see if the flexor rebound augmentation was a constant phenomenon.

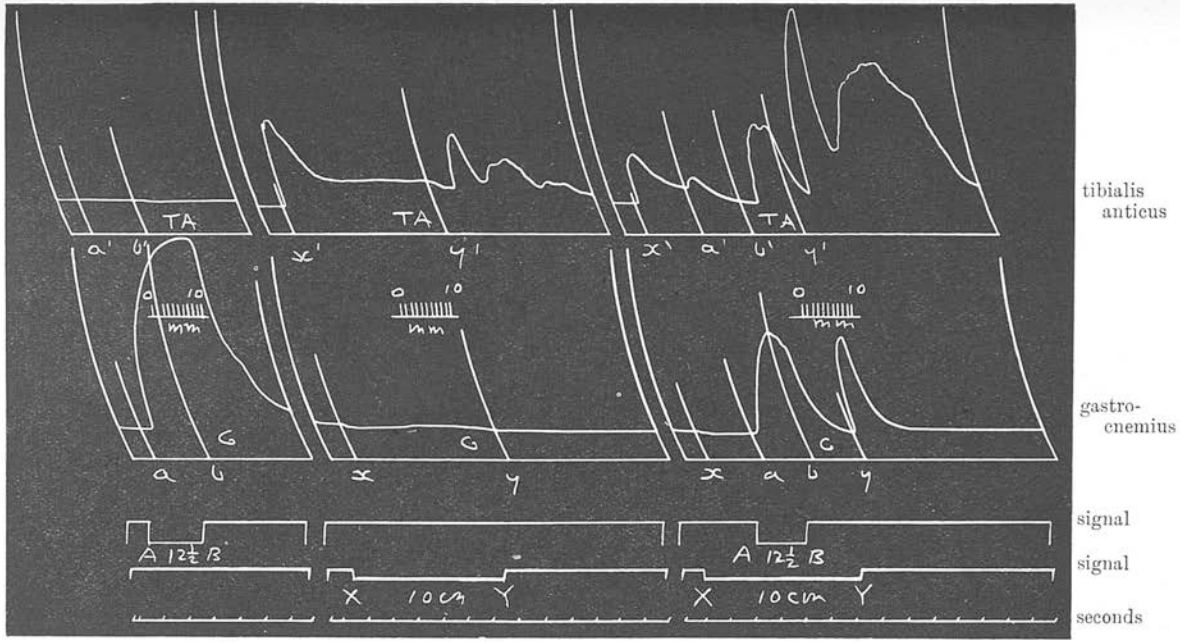


FIG. 10.—Experiment C, clxix., record 301, 7841 ; 28/2/13.—Decerebrate cat. Three reactions obtained 4 hours and 58 minutes after decerebration—minute intervals. A direct continuation of the previous figure and a repetition of reaction *p* in it.

Reaction *q* is a "pure" extension-reflex. The strength and duration of stimulus is the same as that used in the compound reaction (*s*)—and also in reactions *e*, *k*, and *p* in the previous three figures. Note the extensor after-discharge. Extensor terminal relaxation occurs about 2 seconds after cessation of stimulation and is almost complete.

Reaction *r* is a "pure" flexion-reflex. Note the flexor rebound phenomena.

Reaction *s* is compounded of *q* and *r*. In the phase of double stimulation there is a slight preliminary flexor augmentation. This is followed by extensor contraction the extent of which is less than that in the "pure" extension-reflex. In the third phase there is extensor relaxation and flexor augmentation—as before. But here the flexor augmented contraction is continued throughout the third phase. In the fourth phase there is first an extensor rebound contraction, and this is transient—being followed by a marked flexor rebound. This is greatly augmented, and again demonstrates an augmentation of the curious secondary flexor contraction.

This figure therefore again demonstrates an augmentation of flexor rebound when there is an interrupting contralateral stimulus. A repetition of this compound reaction gave the same result—but the flexor augmentation of the third phase was less and gave place to relaxation before the withdrawal of the "background" stimulus. At the same time there was a restitution of extensor contraction at the end of the third phase. The extensor rebound contraction was, as it were, displaced forward into the period of the flexion-reflex.

contralateral interrupting stimuli were applied. With the weakest flexion "background" there was no flexor augmentation in the third phases: the phenomena have already been described in this paragraph. With the intermediate flexion "background" there occurred a slight flexor augmentation in the third phase when the strongest contralateral stimulus was used; and with the strongest ipsilateral "background" there occurred flexor augmentation in all the third phases—this being greater the stronger the interrupting contralateral stimulus. Later in this same experiment these series were repeated and similar results were obtained (figs. 7, 8, 9, 10).

### 3. Where "Extensor Rebound Relaxation" is accompanied by "Flexor Rebound Contraction" in the Terminal Phenomena of the "Pure" Contralateral Extension-Reflex.

"Flexor rebound contraction after inhibition," accompanied by a reciprocal "extensor rebound relaxation after excitation," may occur in the terminal phenomena of the "pure" contralateral extension-reflex of the decerebrate preparation; and in such cases the compound phenomena may be examined.

In the tracing obtained from the flexor muscle in the third phase of the compound reactions of such experiments there is often a sudden augmentation of flexor contraction immediately after the withdrawal of the contralateral stimulus. This almost immediately reaches its maximum and then passes over into flexor relaxation during the continuation of the ipsilateral stimulus. The relaxation, however, is incomplete, and leaves the flexor often at a higher level of contraction than that which obtains at the same point in a "pure" flexion-reflex. The form of this sudden augmentation and relaxation almost exactly resembles that of the flexor rebound contraction after the contralateral extension-reflex. It is, however, of much greater extent; and may be present, and of great extent, when the strength of contralateral stimulus is such that when applied "pure" there is no flexor rebound. The extensor demonstrates reciprocal relaxation. In one instance, with the strength of stimulation used there was no ipsilateral flexion-reflex. It was then found that when the two stimuli were compounded in the usual manner a very large flexor contraction occurred in the third phase. This resembled the flexor rebound contraction of the contralateral extension-reflex in form, but it was of much larger extent.

In these experiments it has so happened that the two antagonistic stimuli have been compounded together in no experiment in which a flexor rebound occurred after the ipsilateral flexion-reflex alone—there has then always been also flexor rebound contraction after the contralateral extension-reflex. But the two stimuli have been compounded at strengths at which of the two the contralateral produced no flexor rebound phenomenon. It was found that here the cessation of contralateral stimulation was followed in the third phase of the reaction by an augmentation of flexion which resembled in form the flexor rebound contraction.

In these experiments it has often occurred that the flexor rebound phenomenon occurred after both the ipsilateral flexion-reflex and the contralateral extension-reflex. It may be noted in passing that such preparations often shew at different times during the taking of long records of reflex reactions the abnormal contralateral flexion-reflex, or approximations thereto. In compounded reactions they also often demonstrate augmentation of flexion in the phase of double stimulation when the ipsilateral flexion-producing stimulus is first applied and the contralateral stimulus then commenced and again withdrawn during the flexion-reflex. When such an augmentation occurs it often again passes over into partial relaxation during the phase of double stimulation, and then, on withdrawal of the contralateral stimulus, there is often a further augmentation of flexion. Towards the end of the period of double stimulation there may appear an extensor contraction, and this then disappears after the commencement of the third phase. In other cases there may be the more usual flexor relaxation during the phase of double stimulation. At the withdrawal of the contralateral stimulus there then occurs flexor restitution of contraction. This may be a rapid movement, and may bring the level of the flexor far above that which would have obtained in the "pure" flexion-reflex. At this level it may persist throughout the third phase until the withdrawal of the ipsilateral stimulus. In such cases the extensor contraction which occurs usually in the phase of double stimulation reciprocally passes over into a relaxation which rapidly becomes complete. In other cases the flexor restitution has at first the form of the flexor rebound contraction which occurs in the same experiment after withdrawal of the stimulus in the "pure" contralateral extension-reflex. Such a rebound contraction may be of a duration of about one second only. Although of the same form, the flexor restitution is of larger extent than that rebound contraction. The relaxation phase is, however, partial only—perhaps of about one-half the extent of the contraction phase—and it leaves the flexor at a level of contraction higher than that at the same stage of the "pure" flexion-reflex. This point having been reached, the flexor begins again to contract slowly, and the wave of contraction may then change over into slight and slow relaxation which persists throughout the remainder of the period of ipsilateral "background" stimulation. In some cases, however, the flexor restitution may be but little higher in extent than the height of the flexor rebound contraction after the "pure" extension-reflex; and, in such cases, it may not bring the level of contraction in flexor restitution up to the level of the "pure" flexion-reflex.

In several experiments series of reactions were obtained in which the strengths of the compounded stimuli were varied.

In one such case [see xv., fig. 12] the contralateral reaction was varied in strength against a constant—but subliminal—ipsilateral "background." Weak "pure" contralateral stimuli gave a maintained extensor after-discharge; medium stimuli were followed by extensor relaxation as the

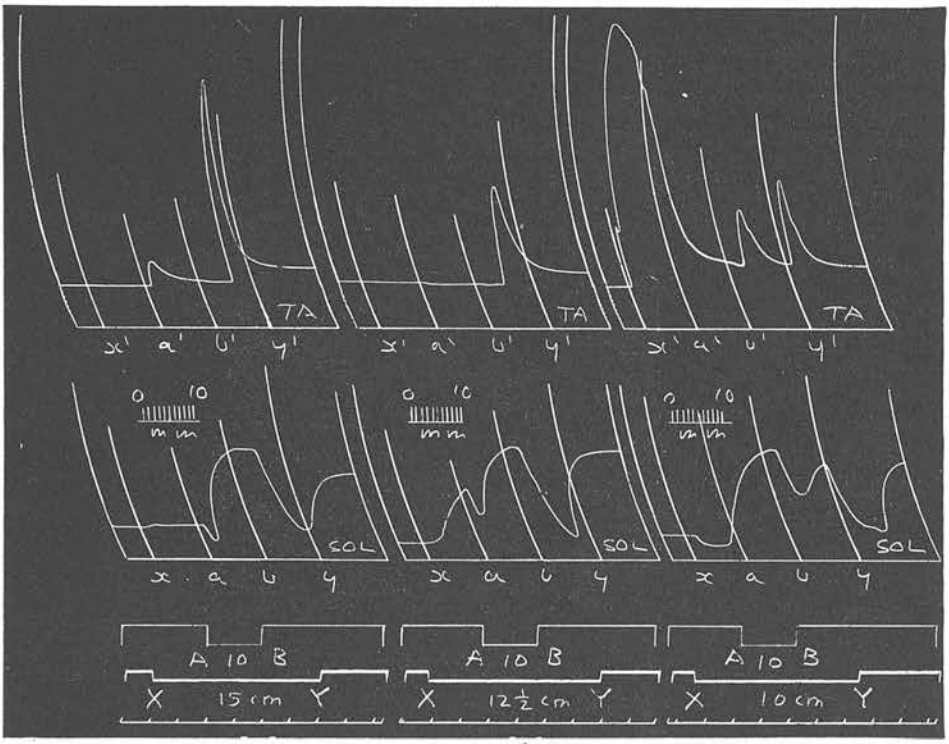


FIG. 11.—Experiment C, clxviii., record 299, 7727; 27/2/13.—Decerebrate cat. A series of compound reactions obtained 5 hours and 8 minutes after decerebration—minute intervals. Here the extensor used is soleus, and not the usual gastrocnemius soleus. The first reaction was obtained 40 minutes after separation of the soleus muscle from the remainder of the extensor group.

Three different strengths of ipsilateral flexion "background" are used, and against them are compounded similar contralateral stimuli. The contralateral stimulus is of the same strength as that used in xv. fig. 12, reaction *g*—8 minutes before.

In *a*—"background" subliminal—double stimulation opens with a transient flexor contraction accompanied by relaxation of extensor tonus. In the "pure" extension-reflex only the relaxation was present—the reciprocal flexor contraction being absent. Thereafter there is extensor contraction. Cessation of double stimulation is followed, comparatively late in the third phase, by extensor relaxation and a marked flexor contraction which is followed immediately by relaxation. In the fourth phase there is an extensor rebound contraction of maintained type.

In *b*—"background" ipsilateral extension—there is no flexor contraction in the phase of double stimulation. Relaxation of the extensor contraction of the "background" reaction occurs, but this does not carry the level of the curve down to the point attained in *a*. Thereafter there is extensor contraction. In the third phase extensor relaxation occurs. It commences sooner than in *a*, but the reciprocal flexor contraction is less. In the fourth phase there is an extensor rebound contraction of maintained type. This is of greater extent than in *a*.

In *c*—"background" flexion—late extensor contraction is just commencing when the period of double stimulation opens. There is no extensor relaxation or flexor augmentation at the commencement of that phase—only extensor contraction and flexor relaxation. In the third phase there is extensor relaxation of less extent than before. This is accompanied by a smaller flexor contraction than before. The extensor relaxation passes over again into contraction, and the flexor contraction into relaxation. In the fourth phase there is extensor relaxation, and for the first time there appears in this phase a flexor rebound contraction. This is transient, and there then appears a late maintained extensor rebound contraction which is of less extent than before.

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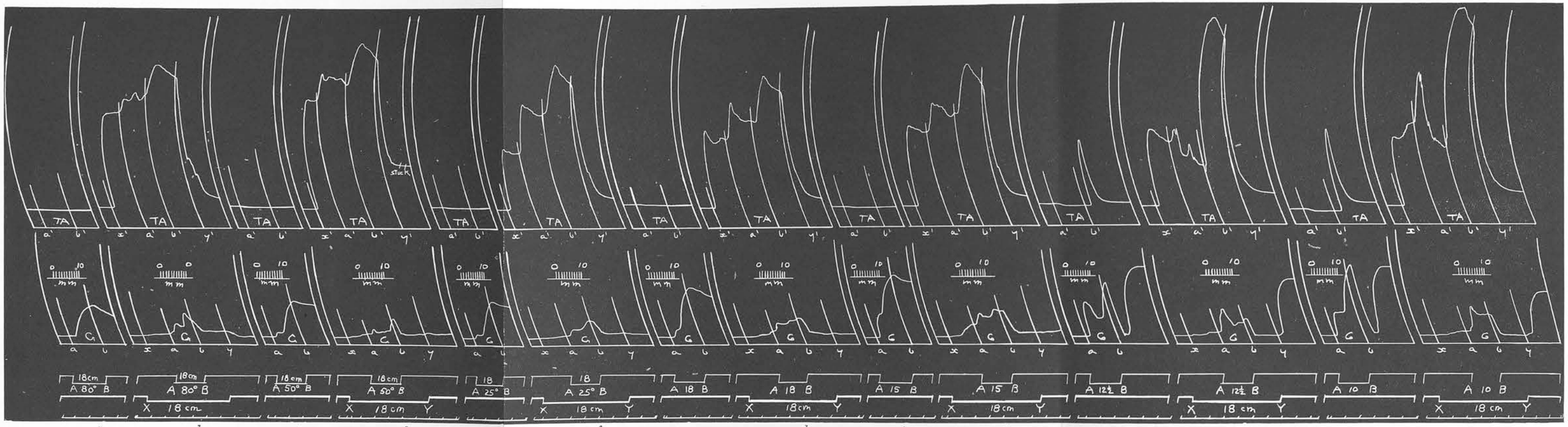


FIG. 12.—Experiment C, clxxv., record 317, 8535 ; 9/5/13.—Decerebrate cat. A series of compound reactions obtained 3 hours and 44 minutes after decerebration—minute intervals.

Reactions *a*, *c*, *e*, *g*, *i*, *l*, and *n* are "pure" extension-reflexes taken with the same strength and duration of contralateral stimulation that is used in each following compound reaction. Of these reactions *a* is the weakest, and they constitute a series in ascending strength. In this series of "pure" extension-reflexes note the appearance of a factor of extensor relaxation during stimulation as the strength of stimulus is progressively increased. In *l* and *n* note extensor terminal relaxation and a reciprocal flexor rebound contraction. After this there is a reconstitution of extensor contraction as a maintained after-discharge. In the other "pure" extension-reflexes there is only slight extensor terminal relaxation.

No "pure" flexion-reflex is recorded. A 6-second one taken a little later shewed a comparatively level plateau—as if the level of flexor contraction in the first phase of any of the compound reactions here had been maintained throughout the reaction.

In the compound reactions (*b*, *d*, *f*, *h*, *k*, *m*, *o*) the "background" of flexion is constant. The immediately preceding contralateral stimulus in each case is used as the interruptor.

In the phases of double stimulation note the augmentation of flexor contraction. This, upon the whole, appears to be of greater extent but lesser maintenance the stronger the contralateral interrupting stimulus. From this it may be argued that the presence of a flexion "background" tends to exaggerate the flexion element in the "decerebrate" type of extension-reflex, and that that element is more pronounced the stronger the contralateral stimulus—whether it is "pure" or compounded against the flexion "background."

In the third phases of the compound reactions (ordinates *b*,*b'*–*y*, *y'*) there is an additional flexor augmentation—which is sometimes very great in extent. This is maintained throughout the phase, and markedly increases with increase in the strength of contralateral stimulation. This seems to point to a similar exaggeration of the flexion element in the terminal phenomena of the extension-reflex when compounded against a flexion "background."

In the fourth phases (after ordinates *y*, *y*) of *m* and *o* there occurs a maintained extensor rebound contraction. This is not present in the other compound reactions (where the contralateral stimulus is weaker), and it was entirely absent in "pure" flexion-reflexes. It is of less extent than the extensor maintained contraction in the terminal phenomena of the corresponding "pure" extension-reflexes. It is of less extent the stronger the contralateral interrupting stimulus—being still less than in *o* in a subsequent compound reaction in which a stronger contralateral stimulus was used (not here reproduced). What is of interest is that the extensor terminal contraction of the contralateral extension-reflex appears to be carried across the third phases of the compound reactions.

terminal phenomenon; and strong stimuli were followed by additional flexor rebound contraction. These phenomena appeared in the third phases of the compound reactions, but were exaggerated for each strength of contralateral stimulation. Thus when a "pure" stimulus gave no extensor terminal relaxation, that yet appeared in the third phase of the compound reaction. When a "pure" contralateral stimulus was followed by flexor rebound, that was greater in the third phase of the compound reaction. Later in this experiment another series, in which the value of the ipsilateral flexion "background" was varied, gave interesting reactions. Here the constant contralateral stimulus when "pure" was followed by a flexor rebound. In the series flexor rebound occurred in the third phases of the compound reactions, but it was smaller the stronger the ipsilateral stimulus. This result—which is contrary to the general rule—is perhaps due to the fact that in the "pure" flexion-reflex there was a marked factor of late extension. This was considerable in the third phase of the compound reactions, and there probably compounded with the flexor rebound of the contralateral stimulus reducing its extent (fig. 11).

In another experiment, against a constant flexion "background," the contralateral stimulus evoked an augmentation of flexion in the third phases of a series of compound reactions. This was greater the stronger the contralateral stimulus, in spite of the fact that a certain amount of deterioration of the flexion "background" occurred in the series. The flexor rebound contraction of the strong "pure" contralateral reaction was of short duration, and followed by a marked extensor restitution of after-discharge; but in the third phase of the compound reactions there was a maintained augmentation of flexor contraction which persisted until the withdrawal of the ipsilateral stimulus (fig. 12).

In another case, where a constant interrupting contralateral stimulus was used with a flexion "background," the strength of which was varied, it was again found that the flexor augmentation of the third phase was greater the greater the strength of the ipsilateral flexion "background" was.

Here the temporal relations of the two stimuli were also varied. The phenomena in the third phase were then rhythmic, and shewed little variation in extent of flexor augmentation. But upon the whole it appeared that the augmentation was the greater the earlier the contralateral stimulus was applied in the period of the "background" ipsilateral stimulus, and it was certainly the case that the element of maintained flexion in the rhythmic phenomenon was greater the earlier the contralateral stimulus fell.

### B. Successive Phenomena after the Discontinuation of the Ipsilateral Flexion-Reflex ["Fourth Phase" of the Compound Reaction].

As in the previous section, we may examine the phenomena first in preparations the reactions of which demonstrate extensor rebound con-

tractions after the contralateral extension-reflex and ipsilateral flexion-reflex.

1. Where "Extensor Rebound Contraction" is present in the "Pure" Contralateral Extension-Reflex.

The extensor rebound contraction may occur as a phenomenon of the contralateral extension-reflex alone at the time of the compounding of the two antagonistic stimuli. In one experiment of this nature a subliminal contralateral stimulus was followed on cessation by an extensor rebound contraction — effective stimuli being followed by "extensor rebound contraction after excitation." At this time the flexion-reflex was not followed by an extensor rebound contraction. When the two stimuli were compounded the termination of ipsilateral stimulation 2 seconds after the end of the phase of double stimulation was followed by an extensor rebound contraction which was of longer duration and greater height than in the case of the "pure" subliminal contralateral stimulus (fig. 13). Later in this experiment the ipsilateral stimulus was followed by an extensor rebound.

In another experiment (fig. 6) a well-marked "extensor rebound contraction after excitation" was present in the "pure" contralateral extension-reflex. Much later in the experiment, and with a greater strength of stimulus than used in the compounded reactions about to be described, there was a slight extensor rebound contraction after the flexion-reflex. At the period when the stimuli were compounded there was no extensor rebound after that reaction. At this time the crossed extension-reflex opened with a very slight flexor contraction which was hardly noticeable, and the extensor rebound on withdrawal of the stimulus was very small. In the phase of double stimulation of the compounded reaction there occurred first an augmentation of flexor contraction; and this experiment was one of those in which the withdrawal of the contralateral stimulus was followed by an augmentation of the flexor relaxation which had again set in during the later part of the phase of double stimulation. This was succeeded again by flexor augmentation of contraction. The termination of the ipsilateral stimulus was followed by an extensor rebound contraction of good extent and well maintained. An ipsilateral stimulus then applied for 6 seconds and uncomplicated by contralateral stimulation evoked a "pure" flexion-reflex which was followed by no trace of extensor rebound. In a series of compounded reactions (fig. 6) the contralateral stimulus was applied for 2 seconds and commenced at different points in a 6-second ipsilateral reaction. When the contralateral stimulus was commenced 1 second before the ipsilateral and terminated after running for 2 seconds—the ipsilateral stimulus then remaining for 5 seconds—there was again no extensor rebound on withdrawal of the ipsilateral stimulus. A very slight extensor rebound (almost unnoticeable) appeared when the two stimuli were applied at the same time and the ipsilateral allowed to run 4 seconds after withdrawal of the contralateral stimulus. The extensor rebound contraction was greater

when the ipsilateral ran for 3 seconds, and still greater when only 2 seconds separated the termination of the contralateral stimulus from that of the ipsilateral. Finally, when the two stimuli were synchronously terminated (the

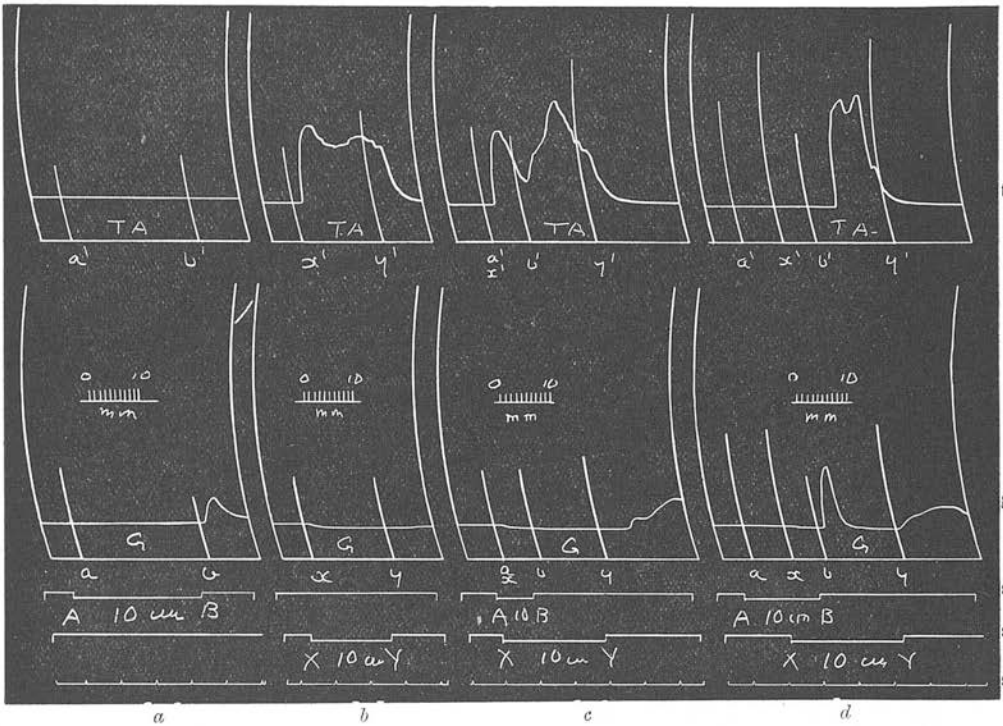


FIG. 13.—Experiment C, cxxvii., record 245, 5708 ; 7/11/12.—Decerebrate cat. A series of reactions obtained 3 hours and 4 minutes after decerebration.

Reaction *a* is a "pure" contralateral one. Note that there is no reaction during stimulation, but that on cessation of stimulation there is an extensor terminal contraction.

Reaction *b* is a "pure" flexion-reflex—note the absence of terminal phenomena save flexor terminal relaxation.

In reaction *c* the two stimuli are compounded together. They commence synchronously, but the contralateral is first withdrawn and the ipsilateral then runs for 2 seconds alone. There is little to note in the phase of double stimulation (1 second), but in the third phase flexor augmentation occurs. On cessation of "background" stimulation there occurs an extensor rebound contraction—although none is present in the "pure" flexion-reflex. This is of greater maintenance than that of the "pure" extension-reflex.

In reaction *d* the stimuli are in "step" arrangement. Double stimulation again is for a period of 1 second, but here—where the reaction commences with "pure" contralateral stimulation—there is no flexor contraction (compare with *c*). The third phase (ordinates *b*, *b'*–*y*, *y'*) commences with a marked extensor contraction of much greater extent then that of the rebound contraction in the "pure" extension-reflex. Thereafter there is an augmented flexor contraction. In the fourth phase there is another extensor rebound contraction, but here it is again of maintained type.

contralateral being then commenced 4 seconds after the commencement of the ipsilateral), the extensor contraction which had appeared during the phase of double stimulation received a sudden augmentation much greater in extent than that of the rebound contractions seen in the previous reactions

of the series. It was considerably greater in extent than the sum of the "extensor rebound contraction after excitation" of the "pure" extension-reflex and the extensor rebound contraction which had appeared after withdrawal of the ipsilateral stimulus in the compounded reactions. In this series the extensor contraction during double stimulation had become a more rapid movement the later in the period of ipsilateral stimulation the contralateral stimulus fell; and an extensor rebound contraction from this had appeared on withdrawal of the contralateral stimulus. This also was greater the later the contralateral stimulus fell—but at the same time was always smaller than in the "pure" extension-reflex.

### 2. Where "Extensor Rebound Relaxation after Excitation" is present in the "Pure" Extension-Reflex.

Even where incomplete extensor relaxation follows upon cessation of stimulation in the extension-reflex, and where there is no extensor rebound in the "pure" flexion-reflex, there may occur an extensor rebound contraction on withdrawal of the ipsilateral "background" stimulus in compound reactions. In one such case (fig. 2) there was no extensor rebound in a "pure" flexion-reflex—where, however, the duration of ipsilateral stimulation was less than that used in the compound reactions. In the extension-reflex relaxation followed upon termination of the stimulus. This was a sharp movement, but incomplete—so that there then remained a certain degree of extensor after-discharge. In the compound reactions an extensor rebound contraction followed the withdrawal of the ipsilateral "background" stimulus. This was greater the stronger the contralateral interrupting stimulus when the temporal relations of the two stimuli were constant, and it was also greater the later the contralateral stimulus fell in the period of the flexion "background" when the temporal relations of the two stimuli were changed. But when the two stimuli were synchronously terminated there first occurred a well-marked flexor rebound contraction, and this was followed by an irregular extensor rebound. The extensor rebound after the compound reactions was not so great in extent as the partial extensor after-discharge of the "pure" extension-reflex.

In another instance [see xv., fig. 13] there was a slight extensor rebound contraction after the "pure" flexion-reflex. This was of very small extent and short duration. In the "pure" extension-reflex there was a partial relaxation on withdrawal of the stimulus. This left a considerable extensor after-discharge. In the compound reaction there occurred a certain degree of persistence of extension in the third phase, and this continued after withdrawal of the "background" ipsilateral stimulus. There was no further augmentation of extension, and the extent of the extensor after-discharge was small, but greater than that of the extensor rebound in the flexion-reflex. It was of course smaller than that of the extensor after-discharge in the extension-reflex.

Where the terminal extensor relaxation of the extension-reflex is complete, a flexor rebound contraction may appear on withdrawal of the ipsilateral flexion "background" in compound reactions even where no flexor rebound contraction appears in the "pure" flexion-reflex when the evoking ipsilateral stimulus (of the same strength as that used for the "background" in the compound reaction) is terminated (see fig. 15).

### 3. Where "Extensor Rebound Contraction after Inhibition" occurs in the "Pure" Flexion-Reflex.

Extensor rebound contraction may occur after the flexion-reflex at the time of the compounding of the two stimuli. In one experiment in which this was the case there was no extensor rebound in the flexion-reflex at the time when the two antagonistic stimuli were compounded, although earlier in the experiment such had been present. When the two stimuli were then compounded there was a distinct extensor rebound contraction at withdrawal of the ipsilateral stimulus. At that time the extension-reflex shewed no "rebound contraction after excitation," and little tendency to tonic extensor after-discharge. A little later a fairly weak contralateral stimulus was compounded with an ipsilateral which gave a strong flexion-reflex. On cessation of the flexion-reflex there was no extensor rebound contraction. Immediately afterwards a stronger contralateral stimulus was compounded with the same ipsilateral stimulus and in the same relations of time. There followed upon the ipsilateral flexion a distinct extensor rebound contraction. The same stimuli were then used, but their temporal relations changed. When the contralateral stimulus fell later in the period of ipsilateral stimulation the extensor rebound contraction which followed withdrawal of the ipsilateral stimulus was greater. The extensor contraction and the flexor relaxation during double stimulation were greater the later the contralateral stimulus fell. A few minutes later the contralateral stimulus was applied late in the period of ipsilateral stimulation. Immediately on the commencement of the period of double stimulation there was a slight augmentation of flexor contraction—which, however, at once gave place to complete relaxation of that muscle. The two stimuli were then synchronously terminated after the contralateral had run for 2 seconds, and the cessation of double stimulation was then followed by a well-marked flexor rebound contraction (fig. 2).

In another experiment there was a good extensor tonic after-discharge after the extension-reflex, and a maintained extensor rebound contraction after the flexion-reflex. On compounding the two stimuli in the usual manner there was a marked extensor rebound contraction after withdrawal of the ipsilateral stimulus. This was of greater extent than that in the "pure" reaction [see xv., fig. 15].

In a third experiment in which the extensor used was soleus alone there was a transient extensor rebound contraction after the flexion-reflex and a

badly maintained after-discharge in the extension-reflex. On compounding the two the flexor was depressed in the phase of double stimulation, and this depression was maintained in the third phase of the reaction, the extensor at the same time slowly relaxing. On cessation of the ipsilateral stimulus the extensor was still partially contracted. This contraction fell slightly, and thereafter the extensor remained in a state of tonic after-discharge which was maintained but was smaller than in the "pure" extension-reflex—there being no augmentation comparable to an extensor rebound contraction [see xv., fig. 13].

In yet a fourth experiment the ipsilateral reaction was one of "decerebrate" type, and there appeared, on cessation of stimulation, an augmentation of the extensor contraction then in being. In this experiment the strength of the ipsilateral stimulus was increased progressively in a series of compounded reactions. Interposed between them, "pure" ipsilateral reactions of the different strengths were taken. In these the extensor rebound contractions were found to be of greater extent the stronger the stimulus was. Cessation of ipsilateral stimulation in the compounded reactions was found always to be followed by an extensor rebound contraction which was of larger extent than in the corresponding "pure" flexion-reflex. At the same time the stronger ipsilateral stimuli were found, in the compounded reactions, to be followed first on cessation by a transient flexor augmentation ("flexor rebound contraction after excitation"), and this was reciprocally accompanied by extensor relaxation. The "pure" ipsilateral reactions taken were usually of 2 seconds duration of stimulation—while the ipsilateral stimulus ran for 6 seconds in the compounded reactions. But in one case the "pure" ipsilateral stimulus was run for 6 seconds. It was then seen that this flexor rebound contraction was greater and the subsequent extensor rebound contraction (which was maintained) was smaller than in the corresponding compounded reaction in which the contralateral stimulus was applied for 2 seconds, and the ipsilateral "background" stimulus for a total period of 6 seconds. In series of reactions in which the strength of the interrupting contralateral stimulus is progressively increased against a constant ipsilateral "background," it may be found that there occurs an extensor rebound on withdrawal of the ipsilateral stimulus, and that this is greater the stronger the contralateral stimulus (fig. 8) [see also xv., fig. 26].

### 4. Where "Flexor Rebound Contraction after Excitation" occurs in the "Pure" Flexion-Reflex.

Compounded reactions in preparations in which the "pure" reactions are followed by flexor rebound contractions may now be examined.

Flexor rebound contraction may occur as a terminal reflex phenomenon in the "pure" ipsilateral flexion-reflex alone. When it does so it may appear after a preliminary flexor relaxation—especially when the flexor contraction during the period of stimulation is badly maintained;

or it may appear as a direct augmentation of the flexor contraction of the period of stimulation—especially when that flexor contraction is fairly well maintained.

In one experiment the flexor rebound contraction after the ipsilateral flexion-reflex appeared after a preliminary flexor relaxation, although the flexor contraction during the period of stimulation was well maintained. When the two antagonistic stimuli were compounded in a reaction, and the contralateral first withdrawn, on cessation of ipsilateral stimulation there was a flexor rebound contraction which was of greater extent than in the "pure" flexion-reflex. This still appeared after a preliminary relaxation of the flexor; but this relaxation was smaller than in the "pure" reaction, and the latency of the flexor rebound contraction was less. A minute later repetition of the compounded reaction again demonstrated flexor rebound contraction on withdrawal of the ipsilateral stimulus. The rebound contraction was of greater extent and duration than before; its latency was less; and there was then no preliminary relaxation of the flexor. Later in the experiment the "pure" ipsilateral flexion-reflex was unaccompanied by flexor rebound contraction. Cessation of stimulation was followed, however, by a flexor after-discharge which sustained the flexor contraction for about 1 second at the level which obtained during stimulation. In a subsequent compounded reaction in which the same strength of ipsilateral stimulation was used there ensued on withdrawal of the ipsilateral stimulus an augmentation of flexor contraction. This flexor rebound was comparatively small in extent; its latency was about 0·3 second; it was interrupted by a partial relaxation which passed over into contraction again before the maximum was reached; and that maximum was attained in about 1·2 seconds. Here a partial extensor relaxation was the terminal phenomenon in the contralateral extension-reflex.

In one experiment "pure" ipsilateral stimuli when weak evoked an abnormal extension-reflex. Stronger ipsilateral stimuli gave a flexion-reflex of "decerebrate" type in which there was at the termination of stimulation a certain amount of extensor contraction; the cessation was then followed by extensor rebound contraction as an augmentation of the extensor contraction then in being. Still stronger ipsilateral stimuli evoked the usual flexion-reflex in which there was little or no extensor contraction during stimulation, cessation of stimulation being followed by an extensor rebound contraction. Yet stronger ipsilateral stimuli—or weaker ones of longer duration—evoked a flexion-reflex which was followed on cessation of stimulation first by a flexor rebound contraction which appeared without intervening flexor relaxation and was accompanied by a reciprocal extensor relaxation; this was followed, in its turn, by an extensor rebound. At this strength of ipsilateral "background" stimulation in a compound reaction the flexor rebound contraction (which still occurred without preceding flexor relaxation) was found to be depressed, and the extensor rebound contraction was found to be augmented, upon

withdrawal of the ipsilateral stimulus. In this instance there was a good extensor after-discharge in the contralateral extension-reflex at the strength of stimulation used in the compound reactions.

It is therefore remarkable that in some cases there seems to be augmentation of the flexor rebound on withdrawal of the ipsilateral "background" stimulus in compound reactions, whereas in other cases there appears to be depression of it. This difference may possibly rest with the nature of the terminal phenomena in the "pure" extension-reflex, for it has been observed that where there is a marked extensor after-discharge in the "pure" extension-reflex there is often depression of the flexor rebound in the compound reaction; whereas when extensor relaxation is the terminal phenomenon in this reflex the flexor rebound may be augmented.

In a case in which there was marked extensor after-discharge in the "pure" extension-reflex and a flexor rebound contraction in the flexion-reflex, the two stimuli were compounded in a series of reactions in which their temporal relations were changed (fig. 1). Here the ipsilateral flexion-reflex was of "decerebrate" type, and there occurred a marked extensor contraction in the latter part of the period of stimulation. Cessation of stimulation was followed by a flexor rebound of good extent and by a marked reciprocal extensor relaxation. In the series of compound reactions it was found that the flexor rebound was reduced in extent, and that this reduction was greater the later the contralateral stimulus fell in the period of the ipsilateral "background" stimulus—that is to say, the shorter the duration of the third phase.

Where there is extensor relaxation as the terminal phenomenon of the "pure" extension-reflex, augmentation of the flexor rebound may occur in compound reactions, and may be greater the later the contralateral stimulus is applied in the period of double stimulation. Thus in one instance the extension-reflex had previously been followed by a marked flexor rebound, but the strength of contralateral stimulation which was used in the compound reactions when applied "pure" evoked an almost liminal extension which was followed by relaxation alone. The "pure" flexion-reflex of the value used in the compound reactions was followed by a very slight flexor rebound contraction. In the compound reactions flexor rebound occurred, and this was of very great extent and duration when the contralateral stimulus fell late in the period of the ipsilateral "background" (fig. 14).

In another instance the "pure" contralateral extension-reflex was followed by extensor relaxation. In the "pure" ipsilateral reflex there had a short time previously been a flexor rebound contraction followed by a maintained extensor rebound; but the flexor element was not present when a series of compound reactions was obtained. The temporal relations of the two stimuli were changed (fig. 15). It was found that when the contralateral stimulus fell early in the period of the flexion "background"

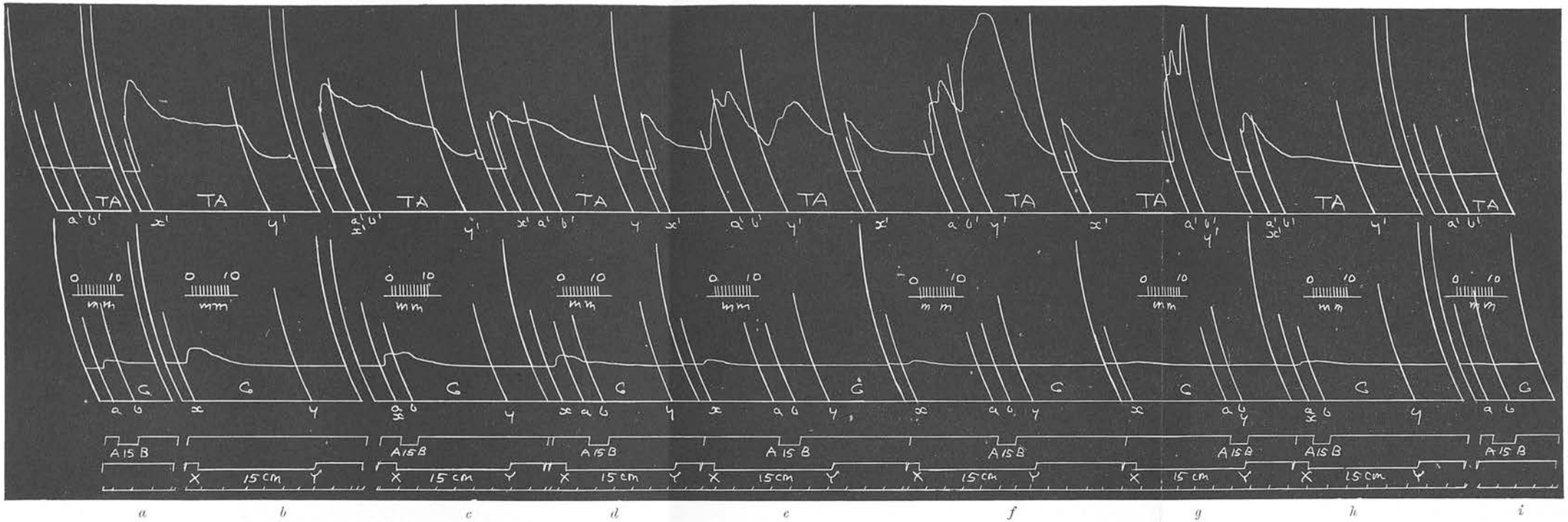


FIG. 14.—Experiment C, clxii., record 290, 7159 ; 17/2/13.—Decerebrate cat. A series of compound reactions obtained 2 hours and 10 minutes after decerebration—minute intervals.

Reaction *a* is a "pure" contralateral extension-reflex of almost liminal value—there had previously occurred flexor rebound contraction in similar reactions. Reaction *i* is taken with a similar strength and duration of stimulation at the end of the series—the reaction is then subliminal.

Reaction *b* is a "pure" flexion-reflex. Reactions *a*, *b*, and *i* are taken with the strengths and durations of stimuli which are used in the compound reactions.

Reactions *c*–*h* are compound—variation of temporal arrangement of stimuli. The interrupting contralateral stimuli first are applied early in the period of the flexion "background," and then ever later. Reaction *h* is a repetition of *c*.

During double stimulation flexor augmentation of contraction appears and becomes ever greater the later the contralateral stimulus is applied. In the third phases there is additional flexor augmentation, and this again is greater the later the contralateral stimulus falls. In the fourth phases there occurs (*e* and *f*) a flexor rebound contraction which is greater the later the contralateral stimulus. (It is not present in the "pure" reflexes.) This is of maintained type. In *g*—where the two stimuli are synchronously terminated—the flexor rebound contraction is not well maintained.

Here the effect of a contralateral stimulus appears to be to augment flexor contraction in the third and fourth phases—and that the more the later it falls in the period of the ipsilateral.

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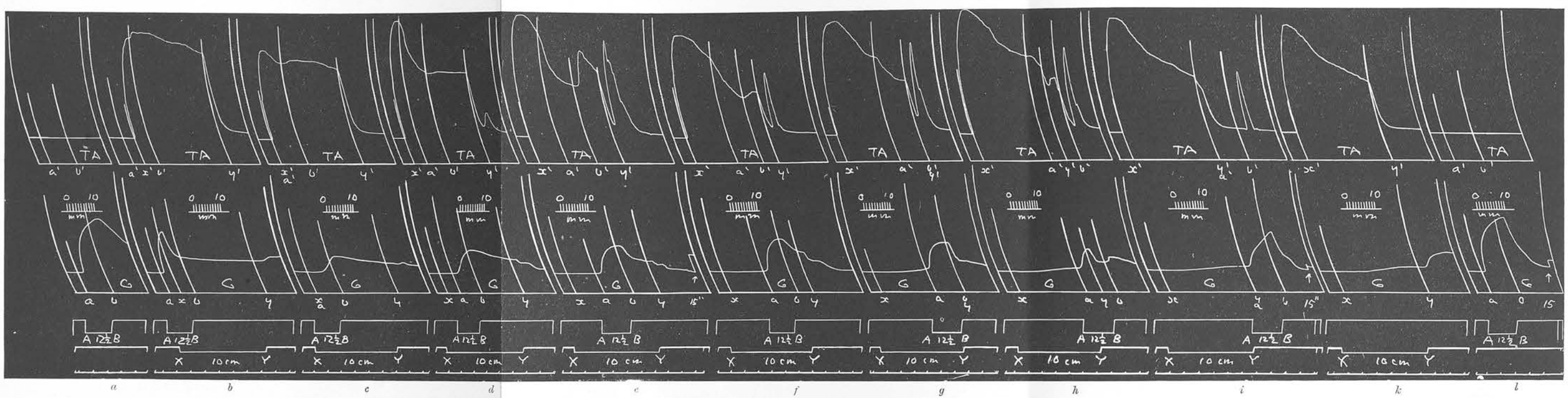


FIG. 15.—Experiment C, clxx., record 302, 7909; 3/3/13.—Decerebrate cat. A series of compound reactions obtained 3 hours and 17 minutes after decerebration—minute intervals. [This figure directly precedes xvi. fig. 21 in time. The two may be compared for differences during double stimulation when different kinds of "background" (same strengths) are used.]

Reactions *a* and *l* are "pure" extension-reflexes—note the extensor terminal relaxation. Reaction *k* is a "pure" flexion-reflex—note the extensor rebound contraction of maintained type. These "pure" reactions are taken with the same strength and duration of stimulation as those used in the compound reactions. Previously the "pure" flexion-reflex obtained at this strength of stimulus had been followed by a small flexor rebound contraction as well as by the extensor rebound.

Reactions *b*–*i* are compound, and the temporal arrangements of the stimuli are varied—the contralateral falling ever later in the period of the ipsilateral "background." In *b* the contralateral stimulus is first applied and first withdrawn—the period of double stimulation lasting 1 second only. In the remaining compound reactions double stimulation lasts for a period of 2 seconds in each case except reaction *h*. In reaction *g* the two stimuli are synchronously terminated; in *h* the contralateral stimulus is allowed to continue for 1 second after the withdrawal of the ipsilateral "background," and double stimulation is for a period of 1 second only; in *i* the stimuli are compounded in temporal succession—the contralateral commencing at the moment of withdrawal of the ipsilateral.

In the phases of double stimulation there occurs flexor relaxation and extensor contraction. The latter is never to the extent which obtains in the "pure" extension-reflex. Note that the extensor contraction and flexor relaxation during double stimulation are greater the later the contralateral stimulus falls in the period of the ipsilateral "background."

In the third phases (ordinates *b*, *b'*–*y*, *y'*) of *b*, *c*, and *d* there occurs a very slow extensor relaxation, and there is a continuation of the flexor depression attained in the phases of double stimulation. In *e* and *f* the extensor relaxation of the third phase is a much sharper act. At the same time there occurs a restitution of flexor contraction.

In the fourth phase (after ordinates *y*, *y'*) of *b* there is a slight extensor rebound. In *c* this is smaller. In *d* there occurs no extensor rebound, but a slight flexor rebound contraction, and this is greater in extent in *e*. In *f* it is smaller, but in *g* (synchronous termination of the two stimuli) again greater. In *h* the third phase is one in which the contralateral stimulus is the "background." Here, on withdrawal of the ipsilateral stimulus (at ordinates *y*, *y'*), there is first a slight flexor relaxation and then reconstitution of contraction. A flexor rebound contraction—which is smaller in extent than that in *g*—now occurs on withdrawal of the contralateral stimulus. Note here the extensor relaxation in the third phase. It is probable that in this reaction the flexor rebound of the ipsilateral stimulus is compounded against the contralateral "background," and that exaltation of the flexion element in the terminal phenomena of the extension-reflex occurs—thus giving the flexor rebound. In reaction *i*—where the two stimuli are in temporal succession—the extensor contraction conditioned by the contralateral stimulus is smaller than in the "pure" extension-reflex. This is the more remarkable in that the "pure" flexion-reflex (*k*) is followed by extensor rebound contraction. There is here a flexor rebound contraction on cessation of contralateral stimulation. This reaction is of interest in its demonstration of extension depression accompanied by exaltation of the flexor rebound contraction. It therefore looks as if the rebound contraction is not necessarily directly connected with the extent of the preceding opposite immediate reflex activity—and the phenomena here may perhaps be explained on the supposition that there continues across the period of the extension-reflex a lasting exaltation of flexion activity which is perhaps of the same nature as that which conditions flexor after-discharge.

This series of reactions exhibits many interesting points. Amongst these may be noted the increase of the flexor relaxation and extensor contraction in the phase of double stimulation, and the flexor rebound in the fourth phase as the contralateral stimulus is made to fall ever later in the period of the ipsilateral flexion "background." It looks as if the extensor terminal relaxation in the "pure" extension-reflex is conditioned by an active flexion element (even although no actual flexor contraction occurs) which cuts short an antagonistic tendency to extensor after-discharge; and that this element compounds with the flexion "background" of the compound reaction and there activates the flexor rebound. While it also looks as if that flexion factor in the terminal phenomena of the extension-reflex may be exaggerated after the flexion-reflex—or that a compounding of the flexion factor in the extension terminal phenomena and of the flexor after-discharge in the flexion-reflex takes place.

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no flexor rebound occurred; but, that when it fell somewhat later, such a rebound appeared. This upon the whole was greater the later the contralateral interrupting stimulus fell. At the end of the series the interrupting contralateral stimulus was applied very late in the period of the ipsilateral "background" stimulus, and the ipsilateral stimulus was first withdrawn. The withdrawal of the ipsilateral stimulus was followed by a slight flexor rebound contraction while the contralateral stimulus was still in being. When the contralateral stimulus was withdrawn in its turn there ensued a flexor rebound which was somewhat smaller in extent than the flexor rebound which had followed in a previous reaction where the two stimuli were synchronously withdrawn. In a following reaction the commencement of contralateral stimulation was made to synchronise with the withdrawal of the ipsilateral—the stimuli thus being in temporal succession. When the contralateral stimulus (which ran for the usual period of 2 seconds) was withdrawn there was a flexor rebound which was smaller again than that in the previous reaction. No flexor rebound occurred on withdrawal of the ipsilateral stimulus, but there was an increase in the duration of the usual phase of flexor relaxation. A "pure" contralateral reaction then taken was followed by extensor relaxation, but by no flexor rebound (fig. 15). In this series it was of interest to note that when the contralateral stimulus was applied early there was an extensor rebound on withdrawal of the ipsilateral "background" stimulus, but that this was not of so great an extent as the extensor rebound which then followed the withdrawal of the "pure" ipsilateral stimulus. In the compound reactions this extensor rebound became smaller and finally disappeared when the contralateral stimulus was made to fall later and later in the period of the ipsilateral.

Where in series of compound reactions the strengths of the antagonistic stimuli are varied, interesting phenomena may be observed. Thus when the strength of the "pure" contralateral stimulus is weak the terminal phenomenon may be an extensor after-discharge; but if the strength of that stimulus is increased an extensor terminal relaxation may appear and may be greater the stronger the contralateral stimulus is.

In an experiment in which this was the case the stimuli were compounded at strengths at which termination of the ipsilateral was followed by a flexor rebound and termination of the contralateral by an extensor after-discharge. In the compound reaction there was then complete suppression of the flexor rebound. A series in which the ipsilateral flexion "background" was constant was then obtained. At the strength of ipsilateral stimulation used the "pure" flexion-reflex was followed by an extensor rebound of maintained form, but this was broken by a small flexor rebound. In the series weak contralateral stimuli were first used, and then the strength of contralateral stimulation was progressively increased. With weak contralateral stimuli there occurred complete suppression of the flexor rebound. Extensor rebound contraction occurred.

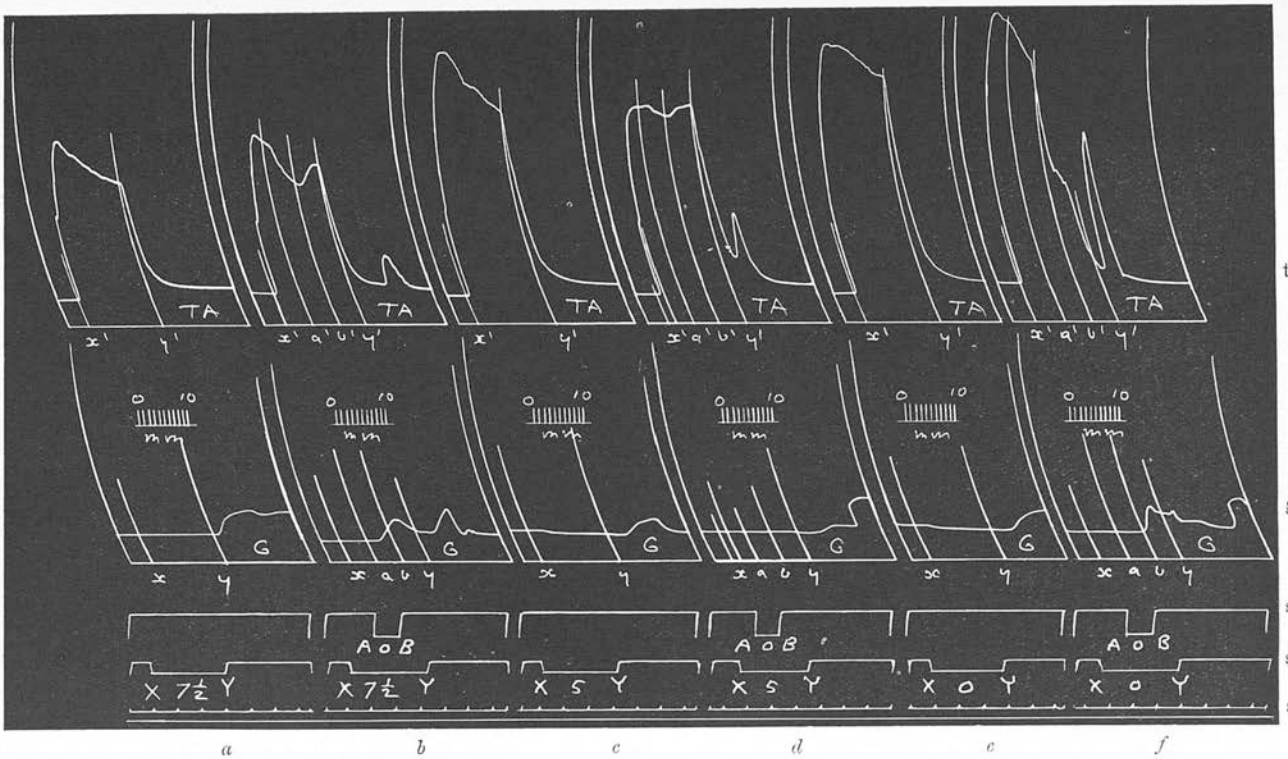


FIG. 16.—Experiment C, clxx., record 303, 7971; 3/3/13.—Decerebrate cat. A series of compound reactions obtained 4 hours and 55 minutes after decerebration—minute intervals.

Reactions *a*, *c*, and *e* are pure flexion-reflexes of three different values, and in each case the strength and duration of stimulation is the same as that used for the "background" in the immediately succeeding compound reaction. Note the extensor rebound contraction—which upon the whole is smaller the stronger the ipsilateral stimulus—and the absence of flexor rebound.

No "pure" extension-reflex is recorded. The reaction at the strength of contralateral stimulation used in the compound reactions was followed by complete extensor terminal relaxation.

Reactions *b*, *d*, and *f* are compound—the strength of the ipsilateral flexion "background" being progressively increased. In *b* note the slight flexor rebound contraction on withdrawal of the ipsilateral stimulus. This cuts down an extensor rebound which had first appeared. In *d* the flexor rebound contraction is of greater extent and shorter latency. A late extensor rebound contraction of maintained type occurs. In *f* the flexor rebound contraction is still greater in extent and of a still shorter latency. It is followed at a greater interval of time by a maintained extensor rebound contraction.

This figure demonstrates the appearance of a flexor rebound contraction as a terminal phenomenon of the flexion-reflex when interrupted by an extension-reflex, and it shews that this may augment with increase in the strength of the ipsilateral stimulus—although that stimulus when "pure" may condition no flexor rebound.

This with the weakest stimuli was slightly greater in extent than that of the "pure" flexion-reflex; with slightly stronger contralateral stimuli it became slightly greater in extent; but thereafter with increase in the strength of contralateral stimulation it gradually decreased. With the stronger contralateral stimuli there appeared flexor rebounds on withdrawal of the ipsilateral stimuli, and these were very much larger than in the "pure" flexion-reflex. Later in the experiment there was obtained a series in which the ipsilateral "background" stimuli were varied in strength, and in which the contralateral stimulus was kept constant (fig. 16). The contralateral reaction at this value was followed by extensor relaxation on cessation of stimulation. Interposed between the compound reactions were taken records of the different "pure" flexion "backgrounds" used. At this stage in the experiment flexor rebound was not observed in any of the "pure" flexion-reflexes, but flexor rebounds appeared in the compound reactions. These rebound contractions were greater in extent the stronger the ipsilateral "background" stimulus was.

### 5. Where "Flexor Rebound Contraction after Inhibition" occurs in the "Pure" Extension-Reflex.

In experiments in which the two antagonistic stimuli are compounded a flexor rebound contraction may be present in the case of the "pure" contralateral extension-reflex alone. In cases in which this, in its turn, is followed by a secondary maintained extensor rebound it has invariably been found that there was no flexor rebound contraction upon withdrawal of the ipsilateral "background" stimulus (see, for instance, fig. 12).

### 6. Where "Flexor Rebound Contraction" occurs as the Terminal Phenomenon both in the "Pure" Flexion-Reflex and in the "Pure" Extension-Reflex.

Flexor rebound contraction may occur as a terminal phenomenon on withdrawal of stimulation both in the ipsilateral flexion-reflex and in the contralateral extension-reflex. In such cases there is, in the phase of double stimulation of the compounded reaction, often a primary flexor augmentation followed by a secondary flexor relaxation. In the third phase—in which the ipsilateral stimulus is running alone—there may be a flexor augmentation which in form resembles the flexor rebound contraction of the contralateral extension-reflex but is of greater extent. This may again give place to partial flexor relaxation during the remainder of the phase; and on cessation of stimulation there may be another flexor rebound contraction. This is then of much shorter latency, and greater extent, than in the flexor rebound contraction of the "pure" flexion-reflex. In one instance in which there was a well-marked flexor rebound contraction after each of the two antagonistic reflexes they were compounded at a time when the micturition and defæcation centres of the lumbar cord were

active. Micturition first occurred and then, for a period of about 10 minutes, there were movements of defæcation. During this period there was a depression of the ipsilateral flexion-reflex but no noticeable change in the contralateral extension-reflex. In the third phase of the compounded reaction there was a restitution of flexor contraction which was of greater extent than the flexor rebound after the extension-reflex, and on cessation of stimulation there was a flexor rebound of much greater latency and of much smaller extent than was the flexor rebound contraction in the "pure" flexion-reflex before this period in the experiment. At the time of taking this compounded reaction there was no flexor rebound contraction after the "pure" ipsilateral flexion-reflex.

In one instance in which there was a rhythmic flexor rebound after the contralateral extension-reflex there was a curious phenomenon in the compound reactions. Here the rebound consisted of two "beats." In the compound reaction a similar flexor rebound occurred on withdrawal of the ipsilateral stimulus, but the "beats" were of greater extent. It looked here as if the flexor rebound of the contralateral reflex had been delayed until after the cessation of the ipsilateral "background" stimulus. Its latency was, however, much shorter. In the third phases of the compound reactions there was a flexor augmentation which was a comparatively slow movement, and was unlike the form of the "beats" in the flexor rebound.

## V. Conclusions and Summary.

1. In this paper the successive reflex phenomena in compound stimulation are examined when the reflex "background" is one of ipsilateral flexion. The "background" stimulus is allowed to continue after the withdrawal of the interrupting contralateral stimulus, and the successive phenomena—as before—are examined in two phases of the compound reaction. These are the "third phase" (in which the "background" stimulus is still in being) and the "fourth phase" (which is that after the withdrawal of the "background").

2. Where the "pure" contralateral extension-reflex is followed by a maintained extensor after-discharge only there may occur in the third phase of the compound reaction a continuation of the flexor depression which obtains in the immediately preceding phase of double stimulation. Where the temporal relations of the two stimuli are varied this depression of the flexor appears to be greater the later in the period of the "background" the contralateral interrupting stimulus falls. This phenomenon occurs when the extensor after-discharge of the "pure" extension-reflex is well marked. Gradual extensor relaxation may occur during the third phase, and it seems probable that the phenomena in that phase are conditioned by an algebraic summation of the flexion of the flexion-reflex and the extensor after-discharge of the extension-reflex. The occasional slight restitution of flexion (followed again by relaxation) at the commencement

of the third phase in these instances may possibly evidence the presence of a slight factor of flexion at the commencement of the extensor after-discharge—one not directly evidenced in the "pure" extension-reflex.

3. Where the "pure" extension-reflex is followed by an extensor after-discharge there may yet occur in the third phase of the compound reaction a partial or a complete restitution of flexor contraction accompanied by extensor relaxation. This restitution may be preceded by an augmentation of flexor relaxation at the commencement of the third phase. This perhaps corresponds to a "flexor rebound relaxation after inhibition" in the "pure" extension-reflex. If the temporal relations of the two stimuli are changed it is found that the flexor restitution of contraction is less the later the contralateral stimulus falls in the period of the ipsilateral "background."

4. Even where the "pure" extension-reflex is followed by an extensor after-discharge, augmentation of flexor restitution of contraction may occur in the third phase of the compound reaction; that is to say, that the level of flexor contraction attained may be greater than that which obtains in the "pure" flexion-reflex. This augmentation seems to be conditioned by the same factors which condition a flexor rebound contraction in the terminal phenomena of the "pure" extension-reflex—although it may occur when there is only extensor after-discharge in that reaction. It looks as if the presence of the flexion "background" could activate a flexion factor in the terminal phenomena of the extension-reflex. The flexor augmentation increases in extent with increase in the strength of the contralateral extension-producing stimulus [but in these circumstances a flexor rebound may occur in the "pure" extension-reflex with increase in the value of the evoking stimulus]. Where flexor augmentation (and not depression) occurs during the phase of double stimulation there is often an additional augmentation in the third phase. The augmentation during double stimulation is often seen where there is a preliminary factor of flexion in the extension-reflex, and the augmentation in the third phase may occur where there is only extensor after-discharge in the "pure" extension-reflex, although with stronger "pure" contralateral stimuli a flexor rebound contraction may appear. In one experiment it was found that the relative value of the flexor augmentation of the third phase (that is, its extent as measured from the level of flexor contraction in the "pure" flexion-reflex) decreased with increase in the value of the "background" flexion-producing stimulus.

5. Where there is only "flexor rebound relaxation after excitation" in the "pure" flexion-reflex no noticeable variation of this has been observed to occur in the "fourth phase" of the compound reaction.

6. Where "extensor rebound contraction after excitation" occurs in the "pure" extension-reflex it may also appear in the "third phase" of the compound reaction. There is then often an increase of the flexor relaxation of the phase of double stimulation at the commencement of the third phase. The augmentation of extensor contraction at the commencement of that

phase is not of so great an extent as that of the extensor rebound contraction in the "pure" extension-reflex. The reciprocal phenomena of extensor augmentation of contraction and flexor augmentation of relaxation in the third phase may be greater the later the contralateral stimulus falls in the period of the ipsilateral flexion "background" in series of compound reactions in which the temporal relations of the two stimuli are varied.

7. Where "extensor rebound relaxation after excitation" occurs in the "pure" extension-reflex the phenomenon may be either partial or complete. In cases where the terminal relaxation in the "pure" extension-reflex is partial it may be found that in the third phase of the compound reaction there persists an extensor after-discharge—which, however, is less than that conditioned by the partial extensor relaxation in the "pure" reflex. At the same time there may be flexor depression. Where the terminal relaxation of the extensor in the "pure" extension-reflex is greater there may yet be only complete restitution of flexor contraction in the third phase, and no augmentation of flexor contraction above the level which obtains in the "pure" flexion-reflex. But more usually this augmentation occurs, and this is especially the case where the "pure" extension-reflex is of "decerebrate" type. Where the ipsilateral "background" is subliminal flexor contraction may appear in the third phase of the compound reaction.

8. If, in these circumstances, the temporal relations of the compounded stimuli are varied, it may be found that the flexor augmentation of the third phase is greater the later the interrupting contralateral stimulus falls in the period of the flexion "background." As then the extensor contraction during double stimulation is found to be greater the later the contralateral stimulus falls, it is possible that this increase of augmentation is conditioned by an increase in the value of the interrupting extension-reflex.

9. If, again in these circumstances, the relative values of the compounded stimuli are varied, it is found that the flexor augmentation is greater the stronger the interrupting contralateral extension-producing stimulus is. The same result seems to occur when the strength of the flexion "background" is increased. Where the flexion "background" is of "decerebrate" type with marked late extensor contraction, in the third phase of the compound reaction there may occur a summation of this extensor contraction with the extensor after-discharge qualified by a partial terminal relaxation in the "pure" extension-reflex.

10. Where there is "extensor terminal relaxation" accompanied by "flexor rebound contraction" in the "pure" extension-reflex, a great flexor augmentation may occur in the third phase of the compound reaction. This may resemble the flexor rebound contraction of the "pure" extension-reflex in form—but is of much greater extent. It may appear—and be of greater extent than the flexor rebound—where the ipsilateral "background" is subliminal. The extensor shews reciprocal relaxation. In these cases in which the flexor contraction phenomenon of the third phase is of the form of the flexor rebound contraction in the extension-reflex there follows, upon

the attainment of its maximum, a partial or complete flexor relaxation. This again may be followed by a secondary and slower flexor contraction during the remainder of the third phase. In other words, the primary flexor movement in the third phase is a di-phasic one and resembles the "beat" of the flexor in rhythmic acts. It looks here as if the transient "beat"-like flexor rebound of the extension-reflex is conditioned by a flexor inhibitory relaxation which cuts short the flexor contraction, and that this inhibitory relaxation may still appear in the complicated phenomena of the third phase—that is, where there is a flexion "background." In these circumstances the relaxation is a later phenomenon (that is, the "beat" is of greater duration), and it is less complete than in the rebound phenomenon of the "pure" extension-reflex. Where the flexion "background" is strong the relaxation may not appear, and the flexor augmented contraction then persists throughout the third phase.

11. In these circumstances, if the values of the two stimuli are varied the flexor augmentation may appear to be greater the stronger the interrupting contralateral extension-producing stimulus. This may be the case where the ipsilateral "background" is subliminal. Where the value of the ipsilateral "background" stimulus is varied it is usual for the flexor augmentation to be greater the stronger the ipsilateral stimulus. In one instance the reverse was observed, and here there was a well-marked element of late extension in the "pure" flexion-reflex of "decerebrate" type.

12. The presence of a flexion "background" therefore appears to augment the flexion factor in the terminal phenomena of the extension-reflex—summation of the two flexions occurring.

13. Where "extensor rebound contraction after excitation" occurs in the "pure" extension-reflex, but no extensor rebound occurs on termination of the "pure" flexion-reflex, there may yet appear in the fourth phase of the compound reaction (that is, on termination of the flexion "background") a marked extensor rebound contraction. Where the temporal relations of the two stimuli are varied this extensor rebound in the fourth phase is found to be greater the later the interrupting contralateral stimulus falls in the period of the flexion "background"—that is, the shorter the duration of the third phase after double stimulation has ceased. As here complete extensor relaxation may occur in the third phase, it looks as if the effect of the interrupting extension-reflex is carried over in such a manner as to influence the phenomena of the fourth phase.

14. Where "extensor rebound relaxation after excitation" is present in the "pure" extension-reflex, and where there is no extensor rebound in the "pure" flexion-reflex, that may yet occur in the fourth phases of compound reactions if the extensor rebound relaxation of the extension-reflex is incomplete. This is greater the later the contralateral stimulus falls in the period of the ipsilateral "background" when the temporal relations of the two stimuli are varied, and also greater the stronger the interrupting contralateral stimulus where their temporal relations are constant but their

relative strengths varied. Where the "extensor rebound relaxation" of the extension-reflex is complete a flexor rebound contraction may appear in the fourth phase of the compound reaction when absent in the "pure" flexion-reflex.

15. Where "extensor rebound contraction after inhibition" occurs in the "pure" flexion-reflex it is found that in the fourth phase of the compound reaction there is also an extensor rebound contraction, and that this is of greater extent than that of the "pure" flexion-reflex of corresponding strength and duration of stimulation. Where the strength of the two stimuli are varied in series of reactions it is found that this extensor rebound contraction is greater the stronger the interrupting contralateral extension-producing stimulus where the ipsilateral flexion "background" is of constant value, and that it is also greater the stronger the "background" stimulus is where the strength of the interrupting contralateral stimulus is of constant value. Where the temporal relations of the two stimuli are varied, but their values kept constant, it is found that the extensor rebound contraction of the fourth phase is greater the later the contralateral stimulus falls in the period of the ipsilateral "background" stimulus. In these experiments this is equivalent to saying that it is greater the shorter the duration of the third phase after the termination of double stimulation.

16. Where "flexor rebound contraction after excitation" occurs in the "pure" flexion-reflex the terminal phenomena of the fourth phases of compound reactions may shew either exaltation or depression of the flexor rebound. These different results are probably conditioned by differences which obtain in the terminal phenomena of the interrupting extension-reflex. Thus it has been noticed that where there is a marked extensor after-discharge in the "pure" extension-reflex there is depression of the flexor rebound contraction in the fourth phase of the compound reaction in which it is used as the interrupting stimulus against a flexion "background." On the other hand, where there is extensor terminal relaxation in the "pure" extension-reflex there is usually exaltation of the flexor rebound in the fourth phase of the compound reaction. It may therefore appear that the terminal effect of the extension component of the period of double stimulation may persist across the third phase of the compound reaction and affect the terminal phenomena conditioned by the withdrawal of the "background" flexion-reflex. The fact that exaltation of the flexor rebound occurs when there is an extensor terminal relaxation in the "pure" extension-reflex seems to point to the conclusion that this terminal phenomenon is a positive one and due to an activity akin to the flexion-reflex which cuts short the extensor after-discharge. Were it due merely to the sudden death of the extensor discharge there would not be expected to occur a flexor exaltation of the rebound in the fourth phase of the compound reaction.

17. Where this flexor rebound contraction occurs after the "pure"

flexion-reflex, and where there is marked extensor after-discharge in the "pure" extension-reflex, it is found that if the temporal relations of the two stimuli are altered in series of compound reactions the depression of the flexor rebound in the fourth phase is greater the later the interrupting contralateral stimulus falls in the period of the flexion "background." This is just what would be expected if the depression of the flexor rebound is attributable to the continued extensor after-discharge factor in the terminal phenomena of the interrupting extension-reflex.

18. On the other hand, where there is extensor terminal relaxation in the "pure" extension-reflex it is found that the exaltation of the flexor rebound of the fourth phase of compound reactions is greater the later the contralateral stimulus falls in the period of the flexion "background" in series of reactions in which the temporal relations of the two stimuli are changed.

19. Where a "flexor rebound contraction after excitation" occurs in the "pure" flexion-reflex, series of reactions in which the relative values of the compounded stimuli are varied may be obtained. In such cases the ipsilateral flexion "background" may be kept of constant value, and that of the interrupting extension-reflex may be progressively increased. This may be done in instances in which weak "pure" contralateral stimuli give extension-reflexes followed by extensor after-discharge alone; stronger "pure" stimuli may give reactions which are followed by extensor relaxation which becomes greater the stronger the stimulus is. In these circumstances it is found that there is depression of the flexor rebound of the fourth phase of the compound reaction when the strength of the interrupting contralateral stimulus is such that when applied "pure" it gives extensor terminal after-discharge. But when its strength is such that extensor terminal relaxation is conditioned in the "pure" extension-reflex, then exaltation of the flexor rebound of the fourth phase of the compound reaction occurs. This is then greater the stronger is the interrupting contralateral extension-producing stimulus. Where in series of compound reactions the strength of the interrupting stimulus is kept constant but that of the "background" flexion-reflex is varied, it is found that the flexor rebound augments with increase in the strength of the ipsilateral "background" stimulus. If the terminal phenomenon of the "pure" extension-reflex is extensor relaxation, and if strengths of ipsilateral stimulation at which no flexor rebound occurs are used, a flexor rebound contraction may yet appear in the fourth phase of the compound reaction.

20. These results are of interest in that they seem to shew that the terminal phenomena of the "pure" extension-reflex are, at any rate in part, of central conditioning. Thus the extension after-effect—which is seen in the extensor after-discharge—appears to be carried over the third phase of these compound reactions (that is, a phase in which extension is suppressed) in such a manner as to influence the phenomena of the fourth phase. And in a similar way the extensor relaxation (flexion) after-effect of the

extension-reflex may be carried over also. It looks as if the flexion factor in the terminal phenomena of the extension-reflex is relatively increased with increase in the strength of the evocative stimulus, and as if the extensor terminal relaxation seen in such cases is due to a positive activity, antagonistic to the extension-reflex, which tends to cut short the extensor after-discharge. A similar activity (but one of opposite sign) probably cuts short the flexor after-discharge of the flexion-reflex. There is a great temptation to make the generalisation that "the activity of a centre (or of a pair of linked 'half-centres') having been tilted in a certain direction tends to remain in the state into which it passes until again tilted by another external force"—or, in other words, that "the discharge of a centre tends to be maintained until cut short by an opposite activity." But some such rule of "central inertia" is probably too sweeping a one, and at present all we can say is that at any rate the activity of extension seems to shew some evidence of it.

21. Where "flexor rebound contraction after excitation" has not been present in the "pure" flexion-reflex, but where "flexor rebound contraction after inhibition" has been present after the "pure" extension-reflex, there has not been observed to occur a flexor rebound contraction in the fourth phases of compound reactions in these experiments.

22. Where "flexor rebound contraction" occurs in the terminal phenomena both of the "pure" flexion-reflex and of the "pure" extension-reflex, it is found that the flexor rebound in the fourth phase of the compound reaction is augmented.